

# The Agaricales in Modern Taxonomy

by

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(Chicago, Ill.).

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fully revised edition  
with 88 plates



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## PREFACE

The fourth and probably last edition of "Agaricales in modern taxonomy" is again fully revised and updated as had been proposed and initiated by the publisher of the preceding two editions, Jörg Cramer, whose untimely death is deeply regretted because mycologists of the world lost an understanding and generous friend. I am grateful that Koeltz Scientific Books undertook the final publication of my book under the present, somewhat difficult situation.

The basic concept and the system of classification have not changed even though some mostly minor rearrangements have been accepted or introduced. Thus, the prefaces to all previous editions are still valid and need not be repeated here.

Changes in the classification from the third to the fourth edition will be evident to the reader if he compares the respective surveys of the genera of Agaricales (3rd ed. p. 161, here p. 154). Aside from the introduction of a few new genera - their number has now risen to 230 - and generic synonyms, the most important changes are (1) the introduction of three suborders (see p. 147), (2) the transfer of *Omphalotus* and *Lampteromyces* to the Paxillaceae, (3) the discussion of the reasons for acceptance or non-acceptance of important proposals published in the period between 1975 and 1985, some as important as those by Kühner (1977-1979).

It is not claimed that the present taxonomy of the Agaricales as here presented is the final and "correct" or only "natural" one. But I honestly believe that it expresses most truthfully the affinities and hiatuses now demonstrable and gives a detailed picture of the status of Agaricales systematics of the present time, without any geographic or theoretical prejudices or limitations. But, as the previous editions, it stresses the author's personal knowledge of the mycoflora of many parts of the earth and recognizes all taxonomically useful criteria now available. It provides keys that reflect the criteria used for the separation of genera and higher taxa to the extent a key can express them - and it is the only work that provides them - but it should be remembered that many supporting facts are offered in the first 24 chapters and in the paragraphs on delimitation of each genus. In the latter the reader will also find data and hints suggesting the existence of unsolved problems worthy of further research.

Other classifications used by or proposed by modern authors have been discussed. Some of these other classifications are merely variations of the one used here. Others seem at first glance very different but are in reality only an expression of different interpretations of the understanding of the hierarchy of taxa and their definition, and/or of the interpretation of the rules of nomenclature. For example, Kühner's classification shows a tendency toward larger genera where genera recognized by most taxonomists today are presented as subgenera while at the same time the higher taxa are often elevated from families to orders etc. (see also chapter XXIV).

If abstraction is made of these differences, it becomes obvious that the well founded modern classifications, including Kühner's, differ only in a few, mostly relatively minor points. There is still ample room for specialists to perfect or correct the classification but it seems to me that the long lists of new combinations in order to adapt the specific epithets to larger or smaller concepts of the genus or to the ever changing rules of taxonomy do not contribute to perfection of the classification but rather contravene the aim of the Code which pleads for "the avoidance of the useless creation of names" (preamble, 1). Useful progress in taxonomy will be achieved only by careful and complete data on newly discovered or now poorly understood taxa, mainly from regions thus far poorly explored and by obtaining more data on more species with regard to the most promising research methods which have thus far only been applied to an insufficient number of species. It is particularly hoped that the research in the future will extend chemotaxonomy to a larger number of taxa, that experimental methods will be improved so that more pairs of taxa, even the obligatory mycorrhizal ones, can be compared with regard to their sexual compatibility; that DNA analysis can be methodically extended to generic taxonomy and that ways will be discovered to add new approaches to the solution of problems.

Thus, the future of Agaricales taxonomy seems bright. Nevertheless, not any single new approach will automatically simplify or accelerate our progress toward a natural system of classification of the Basidiomycetes. Where live material is needed for experimentation or analysis, the methods of the classical taxonomy, careful comparison with the type or authentic or topotype material is necessary, not merely a determination of a taxon by running it down a key. If this problem is not fully understood, errors, wasted time and research resources, and endless controversy will result.

The present edition is the first in which the author has not adapted the naming of the taxa to the newest International Code of Nomenclature but this attitude is not principally based on the impossibility to revise all the names here used without library work lasting many years (and with the expectation that by the time the revision is complete, a new congress will present us with new rules) but because the rule changes since the third edition are detrimental to taxonomical research in Basidiomycetes and the necessary proposals have been made (Proposal 42-44, *Taxon* 33: 745. 1984) to return to a sensible, practical and stable set of nomenclature rules.

## **CRITICAL SURVEY OF THE CHARACTERS OF THE AGARICALES AS THE BASE OF THEIR TAXONOMY**

### **I. THE SPORE PRINT**

The only macroscopical character available that concerns the basidiospores in the Agaricales is the formation of a spore print and its color. This was first emphasized in a classification by Fries. However, Fries minimized (using words like "sordidae" for the description of the spore color), overlooked, or merely ignored certain complications that make it impossible to use his classification, even for an artificial system, without introducing important modifications.

1. *The green-spored group.* This group of agarics, considered as a taxonomic unit in some artificial classifications, belongs in various families and genera in the Agaricales, e.gr. the Agaricaceae, Tricholomataceae, and Boletaceae. The green-spored group has no place in the Friesian classification because Fries misinterpreted either the spore color (in *Phylloporus*), or the species (all the tropical green-spored agarics); it has no place in the modern classification because it contains elements from four different spheres of affinities.

2. *The pink-spored group.* In spite of the combination by Fries of the pink spored agarics in one group and the pink-spored boletes in another, the former is not a homogeneous taxonomic group. The two largest constituents are the Entolomataceae and the Pluteaceae, neither of them related to the other. Fries, and the key-writers following him, especially Saccardo, paid no attention to the fact that there are many other agarics with pink spores, and in order to get to the right genus, in their schemes, it is necessary, as is so often the case, to assume the spores to be white rather than pink. This holds true for such genera as *Rhodocybe* (Entolomataceae), some species of *Clitopilus* (id.), *Phyllotopsis* (Polyporaceae), several common species of *Collybia*, *Lepista*, *Omphalina*, all *Rhodotus*- and all *Termitomycteae*-species (Tricholomataceae) as well as some (few) Amanitaceae and Agaricaceae. As for *Macrocytidia*, see there (p. 472).

3. *The yellow-spored group.* There are numerous species in several genera of "white spored agarics" with cream-colored to ochraceous or citrinous spores but they have passed as white-spored because of errors of observation. Part of the error of the observation was due to the fact that in obtaining the spore print, the pilei were formerly (and still are according to the recommendations of some recent books) put over black or blue paper, the latter in the erroneous assumption that this color did not occur in basidiomycete spores. In order to discover pale colors which are easily misinterpreted as white on a dark background, it is necessary to use paper as pure white as is used and recommended by Crawshay (1930). This is also true for the

paler tints of pink. This group (3) however cannot be separated, on color alone, from pale-spored forms of normally rusty-brown or fuscous brown-spored groups, a phenomenon apparently quite different from the one just mentioned (and illustrated by some species or sections of the genera of Russulaceae, Polyporaceae, Tricholomataceae). These pale-spored species or genera of typically deeper pigmented groups are now supposed to have derived from the latter by a quantitative change (reduction) in wall pigment of the spores. Examples are: Pale (even pallid-) spored species in the Cortinariaceae (*Inocybe*, the genera *Hebelomina* and *Leucocortinarius* as a whole, *Galerina*), the Strophariaceae (some species of *Phaeomarasmius*), the Bolbitiaceae (the whole genus *Descolea* in contrast with *Pholiotina*), the Paxillaceae (one section of *Paxillus*, the whole genus *Hygrophoropsis*), and others. It would be interesting to study the pigments of both groups of yellow-ochraceous spores. There is a phylogenetic implication which would be worth following up: Specialists agree that for example the darker spored Russulaceae are the more evolved, more recent sections of their respective genera (an assumption neither "proved" nor seriously challenged until now\*; they also agree that, for example, the pallid-spored Inocybes appear to be derived from the darker spored majority. If both theses are correct, the direction of evolution in the Agaricales would have been twofold: from the hyaline to the pigmented, and from the pigmented towards the hyaline.

4. *The black-spored ("melanosporous") group.* This group intergrades with the brown and purple-spored groups at certain levels, as has been recognized by Britzelmayr and other earlier writers but many also present some olive tints. The Friesian Melanopsporae fall now entirely into the Coprinaceae with the single exception of the genus *Gomphidius*, which belongs in the Gomphidiaceae, near the boletes. Even *Lacrimaria*, once wrongly incorporated into the purple spored group by Fries, is now considered as belonging to the Coprinaceae. *Melanomphalia*, once placed near *Gomphidius*, shows the basic characters of the Crepidotaceae - except the spore color.

5. *The brown-spored ("ochrosporous") group* is likewise not a homogenous group as was anticipated by Fries. Some genera, in their present, narrowed sense, come close to and form a parallel series with the *Stropharia-Naematoloma-Psilocybe-Melanotus* group, a series so closely related that it is often difficult to separate the corresponding genera and sections of both series. Another series parallels the Coprinaceae in a much less strict manner, and has since been separated from the other Ochrosporae as a family by itself, the Bolbitiaceae. In the Cortinariaceae we have again two parallel series, already partly recognized by Fries; one contains the genera with argillaceous-fuscous spore print such as *Inocybe* and *Hebeloma*, the other the genera with vividly rusty colored spore print such as *Cortinarius* and *Gymnopilus*, both groups tending to develop more pallid-spored side branches or occasional forms (see under 3 above). Brown spores are also found in another non-related group (Paxillaceae).

6. *The gray-spored group* is a much neglected, and at the same time taxonomically unimportant type. Species of *Rhodocybe*, pink-spored in general, are sometimes

\*See comments by Singer & Araujo, in *Beih. Nov. Hedw.* 77: 287. 1983.

found to have distinctly sordid gray spore prints and thin deposits of spores of *Gomphidius* species may appear gray.

7. The light violet-livid color of the spore print of *Pleurotus ostreatus* is characteristic for section *Pleurotus*. It often remains unnoticed if too thin a layer is obtained on other than pure white paper, or else it appears only hours after the fresh spore deposit (which may be whitish or pale cream) has been observed, probably by a certain degree of dehydration. The production of light violet-livid spore print by *Nothopanus eugrammus* has contributed to the transfer of this species and genus to *Pleurotus*, and the occurrence of this color in the spore prints of *Polyporus (Favolus)* has contributed to the acceptance of the thesis that Polyporeae and Lentineae (*Favolus* and *Pleurotus*) belong in the same family. This spore color however is not restricted to the Polyporaceae but occurs in the Tricholomataceae (*Laccaria*), Agaricaceae (*Leucoagaricus*), and Boletaceae (*Meiorganum*).

The above examples show that the spore print colors are not as such indicative of an affinity between groups according to general classes of colors (white, pink, purple, black, brown, etc.). They can be used on the family level only if modified by other correlated characters, and only on a lower level can they be used as the leading characters of taxonomic groups. This shows that Fries' discovery of the spore print colors as a taxonomic character of first grade importance was certainly a fortunate and valuable contribution to the systematics of the Agaricales, however it should be used with reason, without generalizations, and never in a spirit of dogmatic schematism.

The colors observed in fresh spore print are apt to change in the herbarium as a consequence of dehydration. In some cases they loose the olive hue, so characteristic for the spore print of several genera of the Boletaceae, in other cases they bleach to almost white after having been a distinct vinaceous pink in some species of *Tylopilus* (Boletaceae) while in *Russula*, *Melanoleuca*, *Leucocortinarius*, *Pseudoclitocybe* and other "white spored" agarics, the pale colored fresh spore print eventually darkens to decidedly cream color or ochraceous, especially if prepared with some fixative. The opposite phenomenon, viz. the bleaching from pink or light ochraceous to whitish or cream has been observed by this author in *Phyllotopsis* and certain species of *Russula*. In the Gomphidiaceae the fuligineous-fuscous or oliveblack spore print may become deep rusty brown in a few years of preservation. Since many tedious observations by the author since 1945 have shown that the taxonomically important differences are found in the fresh non-dehydrated spore prints, it is necessary to identify the color immediately with the help of a good color chart\*. The pale tints should be rigorously observed on paper of the whiteness of that used in Crawshay's (*I.c.*) plate; the discussion of even whiter ground colors (salts, etc. is rather theoretical than practical.

\*Many mycologists, unfortunately, do not use charts at all but rely on color terms that do not mean the same thing to other people, especially when translated into foreign languages. Some still use Oberthuer, or Klincksieck, but the majority uses Ridgway. *Color Standards and Color Nomenclature*, Washington, D.C. 1912 and Maerz, A. and M. Rea Paul, *Dictionary of Color*, New York, 1930. Second edition 1950. The plates are said to be light-resistant, and besides the number of colors shown is larger than in Ridgway, especially in some colors frequently found in Agaricales. The richest and most vivid colors of spore prints, such as those of *Gymnopilus*, are nevertheless often hard to match in any color chart, and until a

The use of spore prints will probably become more meaningful for modern Agaricales taxonomy if and when precise spectrographic data become available for a sufficient number of taxa.

## II. THE MYCELIUM

### A. Cultural characters

The mycelium has not been used thus far for taxonomic purposes on a large scale. It is obvious, however, that differences of color, zonation, consistency and manner of growth in standard cultures, as employed for polypores by Nobles (1958, 1971) should also be of diagnostic value in the Agaricales. We know that some species of Agaricales have luminescent mycelia. There is now available a rather long list of agarics with luminescent mycelia, a character, with certainty demonstrable only in laboratory cultures. Some species have mycelia with a characteristic odor. This character can be used for the determination of ectotrophic mycorrhiza. The mycorrhiza of *Russula punctata* and *R. dadmunii* has a characteristic odor of iodoform which can be obtained in test tube culture. Other mycorrhizae form allocysts comparable to the pseudocystidia of the carpophores (see below).

Some mycelia form sclerotia (see under B), rhizomorphs (see under B), oidia (or what is called so in the literature on life cycles and sexuality of the Basidiomycetes), conidia, chlamydospores (or chlamydosporoid oidia), oleiferous hyphae (see chapter XIII), and even mycelial basidia, and mycelial cystidia. The latter have been named allocysts by Kühner, a term that should be accepted in view of the original definition of the word cystidia. These allocysts often resemble the cystidia or cheilocystidia of the hymenophore of the same species, or of allied species, but in other cases, they do not remind one of any analogous bodies in the carpophores. A special case of such bodies is represented by the acanthocytes described by Farr (*Mycotaxon* 11: 241-249. 1980) for mycelial cultures of *Stropharia*. They are thorny to somewhat stellate, ± incrusted bodies which can often be found also in the basal mycelium of species of that genus. It is not yet known whether they are characteristic for all species of *Stropharia* or the Strophariaceae.

All these characters have been and will be used for taxonomic purposes as soon as more data become available. The main difficulty here arises from the variance of conditions necessary to grow mycelia of Agaricales, and even so, the mycelia are

special chart for these tinges is published, the mycologist will do well to get the nearest approximately corresponding number, adding "deeper", or whatever the difference may be. The spore prints between pure white and deep ochraceous, such as found in the Russulaceae, *Melanoleuca*, *Chamaemyces*, etc. should be compared with Crawshay's plate (Crawshay, *The Ornamentation of the Russulas*. London 1930) and Romagnesi (1967), last plate.

Unfortunately, later editions of color chart books have a way of deviating, at times rather drastically, from the first. It is therefore necessary to indicate the year of publication of the book used (cf. Singer & Digilio, *Mycologia* 44: 267-269. 1952). The Maerz & Paul (M & P) terms used in the present book are taken from the first edition unless otherwise indicated.

often short-lived and obviously not in normal growing condition. Under these circumstances, a standard method that makes cultures possible and comparable for taxonomic purposes cannot yet be indicated. Most non-mycorrhizal fungi except *Hygrocybe* can be grown on malt agar and on Lutz' synthetic medium, also in liquid media of analogous composition. A widely applicable medium has been indicated by Kühner, and it has been tested, along with many other media\*, by the author. It is a modified Lutz medium\*\*, which appears to be suitable for most non-mycorrhizal species and many mycorrhizal species of the agarics and boletes. The cultures can be started from spores, from the internal tissue of the pileus or stipe, or from the hymenophore (hymenium plus subhymenium). The separation of the pieces to be inoculated should be made under binocular in order to avoid infected places; the interior of young and fresh carpophores is safest in regard to possible contamination. Bacterial contamination is most difficult to avoid in many cases, and separation of the fungus mycelium from the bacteria is not always easy. The culture methods indicated above cannot be applied to certain species of *Amanita* and certain boletes and *Gomphidius*, certain *Cortinarii* and Russulaceae. Their culture requires special techniques, e.g. sterilisation by filtration through a bacterial filter (Seitz or Berkefeld), addition of growth substances, root extracts, etc. In a few cases all attempts at culturing have thus far been unsuccessful. Moser (1966) recommends for *Cortinarius* subgenus *Phlegmacium*, and implicitly for many ectotroph-forming

\*Media other than the Lutz medium, applicable quite generally, are: (1) Kauffman's modified malt extract medium (Wright)

Malt extract	10,0 gr.
Yeast extract	5,0 gr.
Peptone	1,5 gr.
Maltose	5,0 gr.
Magnesium sulphate	0,5 gr.
Calcium nitrate	0,5 gr.
Monopotassium phosphate	0,25 gr.
Agar	30,0 gr.

An optional addendum is dung extract. Add water to 1000 cc.

(2) An excellent liquid medium for shake cultures of Agarics is a Czapek with 1½% yeast extract and 1½% malt extract added and with 1% sucrose. This may also be used as solid medium by addition of agar.

\*\*The formula used by the author:

Water	1000,0 gr.
Difco agar	25,0 gr.
Vitrum's Maltextrakt (Stockholm)	10,0 gr.
Ammonium nitrate	1,0 gr.
Ammonium phosphate	1,0 gr.
Magnesium sulphate	0,1 gr.
Ferric sulphate	0,1 gr.
Manganese sulphate	0,05 gr.

As has been pointed out by A.B. Hatch & C.T. Hatch (*Journ. Arnold Arb.* 14: 325. 1933), the American brands of malt extract are not suitable. The brand obtained from Apoteksvärcentral, Stockholm, Sweden, proved to be superior to American brands in all cases (1948).

agarics and boletes the "BAF"-medium (called so because it contains biotin, aneurin and folic acid):

Maltose	20 g
Glucose	10 g
Pepton	2 g
KH <sub>2</sub> PO <sub>4</sub>	0,5 g
MgSO <sub>4</sub>	0,5 g
FeCl <sub>3</sub>	0,01 g
ZnSO <sub>4</sub>	0,001 g
CaCl <sub>2</sub> 0.1 mol sol.	5 ml
Dico yeast extract	0,2 g
Aneurin	50 γ
Biotin	1 γ
Folic acid	100 γ
Inositol	50 mg
Distilled water	1 liter
Agar (if needed)	15 g

I had occasional success with ectomycorrhizal fungi by adding extract of tomato roots. There were also generally good results with Hagem nutrient agar as modified by Modess, and recommended by Palmer (1971):

Malt extract	5 g
Glucose	5 g
KH <sub>2</sub> PO <sub>4</sub>	0,5 g
MgSO <sub>4</sub> · 7H <sub>2</sub> O	0,5 g
NH <sub>4</sub> Cl	0,5 g
FeCl <sub>3</sub> (1% solution)	10 drops
Distilled water	1000 cc

After autoclaving the pH is 4.6.

I have no evidence that trace elements are essential beyond the impurities in containers and reagents, nutrients and water.

Once the mycelium is in pure culture, it can be used to observe its characteristics under different conditions, or for its capacity to utilize certain N and C sources. This has turned out to be a diagnostic character in *Agaricus*, or a character, as we have seen, related to the ectotrophic character of the symbiosis (if the fungus is symbiotic).

The mycelium may also be used for synthesis with seedlings of mycorrhizal Cormophyta, grown under sterile conditions. It will further serve for inoculation of a parasitic fungus in the host tissue, showing specificity which is likewise a diagnostic character in several cases.

The characteristics of the mycelium may be its capacity to develop certain pigments or sets of pigments, produce a certain odor, or show certain macromorphological and anatomical characteristics.

Unfortunately, and perhaps as a consequence of the difficulties in obtaining a pure culture of many Agaricales, data on the characteristics of the species are still rather scarce, and few species are tested. This is in contrast to the polypores - most of them grown easily - which were studied for a whole set of characteristics in the majority of species occurring in the temperate regions of the Northern Hemisphere. The only group of Agaricales which has been studied thoroughly in this regard, are the Polyporaceae (Polyporoideae), and much weight is given to the diagnostic combination of characters elaborated by Nobles (1958, 1971), see also p. 111.

Regarding the remaining families, only scattered data are available, most of them on the specific level (for example Kühner & Romagnesi's, 1953, and Moser's, 1966, use of pigment color and development in the case of species of *Fayodia*, *Coprinus*, *Cortinarius*, and others).

More recently O. Miller (in Petersen 1971) has studied a number of whitespored gill fungi, and states that the genera *Lentinellus*, *Lentinus*, and *Xeromphalina* have distinct morphological mycelial characters. However, *Lentinellus* is now removed from the Agaricales and *Lentinus* is represented by *L. tigrinus* which is a *Panus*.

Miller uses a cell type scheme for the mycelia he observed in this white-spored group which might be useful to adapt so that in future work a common language can be used. This terminology is borrowed from the one used in Discomycetes:

A. Short-celled tissue:

(1) *Textura globosa*, characterized by round to ovoid cells, thin cell walls, with intercellular spaces, often pigmented. Example: *Armillariella tabescens*.

(2) *Textura angularis*, characterized by polyhedral cells, thin or thick walls, without intracellular spaces, often pigmentless. Example: *Xeromphalina brunneola*.

B. Long-celled tissue:

(3) *Textura intricata*, characterized by interwoven hyphae with spaces between cells, usually thin, hyaline walls. Example: *Cheimonophyllum candidissimum*.

(4) *Textura oblita*, characterized by interwoven or parallel, thick-walled, usually pigmented cells. Example: *Armillariella mellea*.

Chemical reactions were also noted by the same author: *Omphalotus illudens* gives an amyloid reaction in scattered mycelial cells, and in some cases amyloid incrusting material was observed (in relatively low temperatures after 60 days of growth). Gum guaiac reaction was generally deep blue in *Xeromphalina* but the time required for a distinct positive reaction was variable according to species. Aside from these two reactions which may be thought to be generic, most of the other characters are either too wide-spread among the genera of Agaricales, or else only of specific significance. At any rate, too few species have been tested to build up a comparative anatomy of the mycelium useful for taxonomic purposes.

A pure culture is also necessary for studies on the sexuality of the Agaricales (see chapter XXI). In this connection it is often necessary to start from a single germinating spore and later confront the resulting primary mycelia. As for the technique

involved, the reader is referred to Vandendries's papers (see Literature); some interesting technical information can also be found in Kühner's *Recherches morphologiques et caryologiques...* (1946) and Fries & Müller (1984).

Yeast-like (growth by budding cells) stages and stages with diploid hyphal nuclei have been observed in *Asterophora lycoperdoides* (see there) respectively in *Armillariella* aff. *mellea* (see p. 262), and exceptionally in other groups. *Asterophora* and *Armillariella* are thus different from the rest of the Agaricales (as far as known) by a partial return to a life cycle characteristic for Endomycetales.

### B. Characters observed in nature

On the base of the stipe or the point of attachment of the pileus to the substratum, a tomentose or strigose or silky-arachnoid mass or mat of hyphae is observed in many species; in others, white or colored strands of hyphae are macroscopically visible and can be followed through the ground or substratum. In the first case, these mycelial formations are called basal mycelium; in the second case they are known as rhizomorphs. In both cases they are frequently useful characters for the systematist, especially in the Gomphidiaceae, certain Agaricaceae, Boletaceae and Tricholomataceae. A special form of mycelial tomentum formed in advance and independent of the formation of carpophores is the *Ozonium* of *Coprinus radians*\* and some "cyphellaceous" genera.

The mycelial tomentum varies mainly in color, according to the species or variety; also in the degree of development and in consistency. The basal mycelium is entirely absent and the base of the stipe appears to be grafted on the substratum in those species and genera with *insititious* stipe. This character has already been observed by Fries, but has later been disregarded until Kühner (1933, and in later papers) called attention to it again. Sometimes the base of the stipe is surrounded - often unilaterally - by some minute silky mycelial threads, appressed to the substratum (stipe "subinsititious") whereas in the majority of species and genera of the Agaricales an abundant mycelial tomentum, fibrillosity, or strigosity is developed; these strictly non-insititious stipes are usually easily identified as such, excepting the cases where the basal tomentum is obscured by adhering soil particles, or where a pseudorrhiza, a georrhiza, or a basal disc (as in some *Mycenae*) are present.

The rhizomorphs can be subdivided into:

1. True, eventually black, rhizomorphs.
2. White mycelial strands, "thallorhizae" (M. Jaques-Félix 1967).

Though admitting that rhizomorphs are usually constant specific or sectional characters, one will agree with De Bary who says (1887, p. 22) "that the formation of strands is not necessarily found in all the species that belong to the cycles of

\*Excepting the *Ozonium*, we can synonymize the basal mycelium with Fayod's "mycelium secondaire" or De Bary's secondary mycelium, a terminology which has now been abandoned since the secondary mycelium in Basidiomycetes has a cytological connotation (see chapter XXI)

affinity indicated [by their family and generic names]; on the contrary, it may be wanting in one of two nearly allied species, and be found in the other".

One should avoid confusing true black rhizomorphs with sterile stipes - which is rather easy in certain species of *Marasmius* where the formation of the pileus is frequently delayed or suppressed so that interfering dry or cold spells will tend to cause sterility of the carpophores. The stipes, then, appear etiolated and white-tipped. Such sterile stipes in marasmoid fungi have been described, particularly in subtropical and tropical species, as criniform or "crins" (M. Jacques-Félix), but they are apparently not basically different from what M. Jacques-Félix (1968) has called "télèpodes" in *Polyporus rhizomorpha*. Certainly, the sterility of the stipes is not restricted to the marasmoid fungi but it would appear that the antler-like formations observed in *Lentinus lepideus* and *Panus tigrinus* - often caused by lack of light - are of the same general category. It would seem that in all those forms which instead of a button first form a long stipe with the pileus primordium, in contrast to the stipe which is geotropic and dependent on higher light intensity (Taber in Sussman 1966), the tip of the stipe may fail to develop a pileus, and a criniform stipe or "télèpode" may result.

Other formations of the mycelium are: the pseudosclerotia, sclerotia, perennial pseudorrhizae, cryptas, mycorrhizas, and sterile carpophoroids. The latter will be discussed in subsequent chapters since they are rather a modification of the seasonal basidiocarpous formations as a whole whereas the others are not in any way homologous with the carpophores and can rather be characterized as special organs where primary functions are either long term resistance, storage of food material, or exchange of nutrient substances with the rootlets of the mycorrhizal symbiont. In the first category belong: black rhizomorphs, in the second - sclerotia, perennial pseudorrhizae, and in the third - the cryptas and mycorrhizae. The pseudosclerotia are probably without function and merely a result of processes of extracellular assimilation of substratum with a certain dense hyphal growth in a well circumscribed sphere of the mycelium.

There are, therefore, the following four groups of mycelial formations:

1. *The pseudosclerotium*. This is a mass of substratum (mineral or humus particles, or wood) held together by the mycelium so as to form definitely circumscribed bodies resembling sclerotia. Such formations are characteristic in *Polyporus tuberaster*, *Panus fulvus* (Pl. 5).
2. *The sclerotia, perennial pseudorrhizae, and the black rhizomorphs*. The sclerotia are usually bulbous or ovoid-ellipsoid to globose bodies, either immersed or superficial; the perennial pseudorrhizae are rootlike hypogaeous bodies which are vertically elongated; the black rhizomorphs are horse-hair-like filaments. Sclerotia are found *i.al.* in *Pleurotus tuber-regium*(Pl. 4) where they are very large, in *Agrocybe tuberosa* (medium sized), and in three *Collybiae* where they are small.

Sclerotia (mycelium persistants tuberculeux) have been subdivided by De Bary (1884) and Fayod (1889) into mycelial tubercles, exosclerotia, and endosclerotia. The latter have not yet been found in Agaricales. However, the first two types are

represented in this order. Mycelial tubercles are those sclerotia "where one can oppose to their morphological base one or several points from which the stipes of the carpophores rise at germination" (Fayod 1889). As an example of this kind, Fayod indicates *Collybia tuberosa*. In the exosclerotium no such points of germination are present, and any cell or group of cells in the cortical layer of the exosclerotium is apt to produce carpophores; yet, their morphological base (the "hilar" end) is usually recognizable all through its development. Such a sclerotium is formed by *Coprinus stercorarius*, *Collybia racemosa*, and *C. cookei*. It is surprising to find both types represented in one single section of *Collybia*.

The *Pachyma*-type (called *Mylitta*-type by some) of sclerotia is conspicuous because of its large, often enormous, size and ± hypogeous development. The carpophores are eventually formed on the upper surface of the sclerotium. The same type of sclerotium is formed by species of *Polyporus* and *Pleurotus*, a fact contributing to the present circumscription of the family Polyporaceae.

Perennial pseudorrhizae or sympodia have been studied by Buller (1934). They represent the perennial base of the annual portion of the carpophores, branching underneath in the earth and close to or inside the substratum into several individual annual carpophores. The sympodium may be aerial in *Marasmius arborescens* according to M. Jacques-Félix (1967). A special term is necessary for the annual pseudorrhizae since these are merely a subterranean (or submerged) part of the carpophore, more precisely the stipe, and often exist alone, i.e. directly rising from the mycelium rather than from a perennial pseudorrhiza. Such a term has been proposed very recently by M. Jacques-Félix (1967): geopodium ("géopode") which is defined as the part of the stipe which is submerged in the earth (or substratum). This geopodium may appear more or less root-like ("radicant") (less so in some dune-inhabiting fungi, more so in such species as *Oudemansiella radicata* or the *Strobilurus* and *Phaeocollybia* species (Pl. 44).

3. *Cryptas* are sleeve-like formations around tree roots (especially *Coffea*, *Citrus*, and others) in tropical and subtropical conditions. These organs of the fungus provide shelter for certain scale insects living on the root-surfaces of these trees. They are the morphological expression of a strange and highly complicated coexistence of various organisms, partly in symbiosis, and partly in a parasite-host relationship.

4. *Ectomycorrhizae* are more tender structures consisting of mycelial hyphae enveloping (the "mantle") only the thin rootlets of certain trees, with which they live in ectotrophic mycorrhizal (symbiotic) relationship, forming a complex organism - the ectotroph (consisting of the mycorrhizal fungus + the mycorrhizal tree, in a way comparable to the lichen consisting of the lichenized fungus and the associated alga). The hyphae of the fungus enter the intercellular spaces of the rootlets whereby in a section they appear to form a network of hyphal strands among the cells which is known as the "Hartig-net". Usually, the hyphae do not penetrate the cell-interior (as they do normally in endomycorrhiza), but will do this exceptionally (so-called ectendotrophic mycorrhiza). A list of phanerogams which form ectomycorrhizae with ectomycorrhizal fungi has been published by Singer & Morello (1960); to this

list we may now add *Eucalyptus* and *Leptospermum* (Leptospermaceae) *Shorea* (and probably most genera of Dipterocarpaceae) Pl. 44) some Leguminosae especially Caesalpiniaceae, and *Glycoxylon* (Sapotaceae), *Gnetum* (Gnetaceae) as well as a number of probably facultatively mycorrhizal (ectomycorrhizal under certain ecological conditions, generally non-ectomycorrhizal in others) plants such as certain Ericaceae (*Arctostaphylos*, *Arbutus*) several leguminous trees (e. gr. *Inga*, *Paramacrolobium*), *Allophylus* (Sapindaceae), *Psychotria* (Rubiaceae) *Neea* and *Torrubia* (Nytaginaceae) and other trees and shrubs known to form so-called cicatrizing mycorrhiza in the tropics and subtropics. But the trees which are constantly mycorrhizal by an ectotrophic relationship, as long as they grow in their natural habitats, belong to the families named above and the Pinaceae, Salicaceae, Fagales, and to the genera *Tilia* and *Fraxinus* (not all species of these), *Coccoloba* (Kreisel, *Biol. Rundschau* 9: 97. 1971) and *Polygonum* (the last perhaps facultative). Some Rhamnaceae and Rosaceae (Moser, *Mitt. forstl. Bund.-Vers.-Anst. Wien* 75: 362) are facultatively ectomycorrhizal with Agaricales.

Furthermore, Singer & Morello have given a list of the fungi entering obligatory ectotrophic mycorrhizal relationships. These belong in some groups of the Gasteromycetes, Agaricales, and Aphyllophorales. Some groups of these orders are constantly ectomycorrhizal and incapable of surviving for a long period without the presence of at least a facultatively mycorrhizal higher plant - a relationship explained by the lacking or reduced capacity of the fungus to utilize polysaccharides which tends to make it dependent on the utilization of the simple carbohydrates produced by the Cormophyta. Other groups of the same orders complete their life cycle always (anectotrophic organisms) or often and potentially in continuity (facultative ectomycorrhizal organisms) without association with living Cormophyta. We have here an ecological and physiological character which may be and has been utilized for taxonomic purposes in the same order as parasitism can and will be used for taxonomic purposes. In a natural classification, obligatory ectomycorrhiza is not a random character, but related species behave in a similar manner (Singer 1950). For this reason, this character is indicated in the Special part of this book for all genera. The methods of determining whether a species is obligatorily ectomycorrhizal have been described in the literature on mycorrhiza. Originally, it was thought that experimental methods viz. synthesis, or direct observation (excavating mycelial strands leading to the tree roots) are sufficient to provide scientific proof. We know now - as this author has shown in several papers on the subject - that synthesis does only show a potential capacity of the fungus to form ectomycorrhiza, and direct observation is often impossible or inconclusive. It should therefore be understood that the first and essential step should be the determination of obligatory ectomycorrhiza in each species by ecological-phytogeographical examination as pointed out first by Singer & Morello (1960), and that rootlet anatomy and synthesis will be further, confirmatory steps. Generalizations (made in the most cautious manner) and direct observations in the field will help to single out those groups of fungi which are *probably* ectomycorrhizal and it will thus be possible to restrict more detailed observations by more refined methods to those fungi where a strong suspicion of ectomycorrhiza leads to inclusion in the

list of probably ectomycorrhizal fungi (such as has been published by Trappe since 1960, L.N. Vassilieva 1973, Singer, Araujo & Ivory 1983, and others). Unfortunately, what we know about ectomycorrhiza formed by Ascomycetes is still difficult to interpret. But it would seem that Ascomycete mycorrhiza which appears to be morphologically similar to ectomycorrhiza is physiologically somewhat different from typical ectomycorrhiza since a true mutual symbiosis is apparently not achieved, and the relationship might fit into the category of pseudomycorrhiza. But this question does not concern us here. The facultative ectomycorrhiza, formed on Cormophyta capable of producing short-roots and receiving mycelium of ectotroph-forming fungi by such species whose mycelium has the capacity of utilizing carbohydrates in the form of polysaccharides and being otherwise facultatively independent of the life processes of the Cormophyta is formed by fungi which often grow in areas completely free of ectotroph-forming Cormophyta.

Among the Agaricales, we find such species in the genera *Laccaria*, *Lyophyllum*, *Leucopaxillus*, *Paxillus*, and others.

5. *Endomycorrhiza*. Agaricales are also involved in the formation of another type of symbiosis in which the mycorrhizal fungus enters the root or other organs in search of cellulose or lignin - which it is capable of utilizing as principal carbohydrate source by entering the interior of the cells of Cormophyta, often forming haustoria-like hyphal ends which are eventually digested by the higher plant. Endomycorrhiza is a "catch-all" term simply based on the morphology of the hyphae entering the cells, but among the phenomena to be listed under this heading, there are a few well defined and characteristic types of mycorrhiza, and among these we know most about the orchid-mycorrhiza in which representatives of the Agaricales also participate. Those Agaricales which form orchid mycorrhiza and those which form typical ectomycorrhiza are always mutually exclusive. In other words, fungi which form orchid mycorrhiza belong in groups taxonomically different from those that form ectomycorrhiza. As far as we know now, species of *Armillariella* and *Gymnopilus* (Pl. 1, Fig. 1) are most certainly involved in orchid mycorrhiza, and so is a tricholomataceous fungus described by Ade as *Xerotus javanicus* (exact generic position unknown, but certainly not a *Xerotus* = *Xerotinus*\*). There are probably numerous species of Basidiomycetes including Agaricales, and their imperfect stages, which should be listed in this context. But any taxonomic value in this physiological character is unlikely inasmuch as it seems to be established that none of the species now known to form orchid mycorrhiza do so as an obligatory or even beneficial part of their life cycle. Thus, *Gymnopilus aculeatus* shown by me to form orchid mycorrhiza with *Cattleya* in a Massachusetts greenhouse, occurs frequently without the presence of epiphytic orchids, growing saprophytically and perhaps parasitically on a wide range of different Monocotyledones.

Both ectotrophic and orchid mycorrhiza with participation of certain Agaricales is enormously important in silviculture, succession-studies, quantitative appraisal of eco-systems in forested regions, historical plant geography, and nature conservation.

\*Probably a *Gerronema* (see H. Burgeff, Saprophytismus und Symbiose. G. Fischer, Jena 1932, pp. 156-157).

### III. LICHENIZATION

Lichenization is the phenomenon of alga-fungus association whereby a symbiotic (or "helotic") relationship and a close anatomical aggregation in a usually constant pattern obtains. If this association is the normal condition of the respective fungus in nature, the resulting complex organism is a lichen.

Agaricales have only recently been mentioned as forming lichen combinations. The first to indicate certain Agaricales as lichenized was H. Gams (1962). He showed that in particular the lichen genera *Botrydina* Brébisson and *Coriscium* Vainio are basidiolichens, and he added that he had observed *Omphalia* species associated with these lichen thalli. Further observations confirmed that species of the omphaloid genera *Omphalina* and *Gerronema* are indeed the fruiting bodies of these lichen thalli (Poelt & Oberwinkler 1964; Heikkilä & Kallio 1966; Poelt & Jülich 1969; Singer 1970; Oberwinkler 1970) whereby in the *Botrydinae* the fungus is associated with *Coccomyxa subellipsoidea*, *C. pringsheimii* and *C. spec.*, in the *Coriscium*-type with *C. icmadophila*.

From all these observations it would appear that the association of certain species of *Omphalina* and *Gerronema* with green algae is the normal condition in which these species are found in nature. But is a specific link between certain species of fungus carpophores with certain species of algae and lichen thalli constant? Singer (1970) showed that in the case of *Gerronema hudsonianum*, the holartic alpine-arctic-subarctic form (= *O. luteolilacina* Favre), associated with *Coriscium*, differs in its lichenization from the South American Andine form which is associated with *Botrydina* while in the case of *Gerronema alpinum* it is the European form which is associated with *Botrydina*, and the South American Andine form with *Coriscium*. The conclusion is, at present, that there are physiological-geographical races in both species of *Gerronema*. *Gerronema fibula*, however, also indicated by Gams as forming lichens of the *Botrydina* type, has, during a systematical search in 1970-71, never been found lichenized (Singer & Clémenton 1972), nor have all other species of *Omphalina* or *Gerronema* the same association. However, I have been able to corroborate another association: *Omphalina rustica* is constantly associated with lichen thalli of the *Botrydina*-type (Poelt & Jülich 1969; Singer & Clémenton 1972) and *Marasmiellus affixus* is likewise lichenized in Australia, with a *Coccomyxa* spec. as algal component (Singer 1972). *Lactarius igapoensis* is also found associated with algae.

Under these circumstances one cannot but agree with Donk (1964) who says that "it would seem rash to put all phycophilous species of Clavariaceae into a distinct genus merely on account of their phycophily, first because some of them seem to be allied to non-phycophilous species and secondly because of several possible related species the phycophily may be suspected but has not yet been confirmed or has even been denied", a statement that may also be acceptable for the genera of Agaricales involved.

Consequently, the lichenization as such, and the different types of lichenization should not be considered primary diagnostic characters in generic taxonomy. On the

other hand, it cannot be denied that lichenization is a character of some significance, on the same level, as mycorrhization. This is obvious from the fact that it seems to occur in two genera which, also on morphological grounds, are closely related, viz. *Omphalina* and *Gerronema* (*Omphalinae*).

#### IV. CARPOPHOROIDS

Carpophore-like formations with a gasteromycetoid appearance and formed at the same time instead of or as forerunners of the normal capophores, consisting of sterile hyphal tissue similar to that of the normal carpophores but either entirely sterile or with noticeably reduced fertility, and without visible function, have been observed in various groups of the Agaricales and are known as carpophoroids (Singer 1951). It is not clear at present which factors determine this change in the development of an agaric or bolete fructification in every case. It may be assumed that absence or scarcity of light in a certain early stage of development either directly causes physiologically or triggers a minor mutation which leads to the development of carpophoroids. In some cases - *Psilocybe mexicana* "sclerotia" (= carpophoroids), studied by Heim et al. 1958) - light has been shown to have a decisive role. In the case of *Entoloma (Acurtis gigantea)*, it has been suggested that the carpophoroid condition is caused by parasitizing *Armillariella* aff. *mellea*, an assumption thus far not proved experimentally but, on the basis of Watling's and my own observations quite defendable inasmuch as basidiospores borne on endobasidia are frequently observed in sections of the *Acurtis*. The fact that carpophoroids are known only in Agaricales combined with their gasteromycetoid appearance and lost functionality, has contributed to the tentative interpretation of carpophoroids as being a phenomenon of retarded development - a return to an earlier, simpler type of fruiting-body development. This is in agreement with the theory which postulates a derivation of the Agaricales from certain Gasteromycetes (see chapter XXIII). At any rate, the carpophoroid, either as a normally dimorphic alternate type or an exceptional formation, develops from a primordium which, when maturing, fails to ever achieve the last (agaricoid) stage of its individual development after it has reached the endocarpous stage or before it forms an exposed hymenium.

Such individuals may be extremely rare and might be considered aberrations or "monstrosities" (a rather vague term at best); or else they may be occurring regularly with or instead of the agaricoid or boletoid fully fertile carpophores. In some cases there are transitions between normal fruiting bodies and carpophoroids, for example in cases where aside from typical carpophoroids and typical agaric carpophores intermediate formations are observed which show some traces of an externally formed hymenium with basidiospores typical for the genus. In other cases we observe transitions from typical carpophoroids to protocarpic tubers. Here the normal carpophores will in some instance, be formed by a later, secondary proliferation from a carpophoroid basis, i.e. some carpophoroids of a carpophoroid population will eventually "germinate" to form perfect carpophores much in the way some sclerotia are known to do.

Typical carpophoroids are observed in *Entoloma giganteum* (Pl. 7), *Mycena micromphala*, several species of *Marasmiellus*, a mutant of *Lentinus edodes* (Iwade 1944), in *Boletus caribaeus* (Sing.) Sing., and in *Tylopilus rubrobrunneus* Mazzer & Smith. The gigantic tubers which have been found in cultures of *Agaricus bisporus*, race 59 c of Fritsche & v. Sengbusch 1963 (cf. Reijnders 1977) may belong here. If so, we have at hand an organism which might facilitate further research on the conditions favoring carpophoroid formation.

## V. GASTEROMYCETATION

The term gasteromycetation has been chosen to characterize a tendency of some species of Agaricales to form carpophores - fully fertile and anatomically and chemically as well as cytologically in agreement with the normal or mother form - but assuming or retaining the shape of a Gasteromycete. Such carpophores may also be defined as fully fertile carpophoroids but cannot be classified as such because they are not "false carpophores" or "seemingly carpophores" but they are carpophores to the same degree as the non-gasteromycetoid ones.

Gasteromycetation tends to produce carpophores with gleba-like hymenophore insofar as the hymenium is formed inside of irregular ducts or loculi whereby the spores, at maturity, have no free outlet by vertical fall. Thus the hymenophore is analogous and very similar to that of *Secotium* or *Hymenogaster*. Nevertheless, the configuration of the basidia and sterigmata and spores as well as the sporogenesis as a whole is that of a typical agaric.

Here again, the origin and function of such carpophores is not fully clear. In some cases (*Psilocybe* spec., studied by McKnight; *Lentodium*-forms of *Panus tigrinus*, studied by Rosinsky & Robinson) small mutations have taken place which can be induced by certain conditions of the primordial growth (darkness or inundation should be considered as possible or probable factors inducing such mutations). In both these cases - the only ones rather well known - a certain analogy with carpophoroid-producing related forms cannot be denied. The only difference between McKnight's *Psilocybe* and the *Lentodium* forms on one hand and *Psilocybe mexicana* and *Lentinus edodes* f. *sterilis* on the other, lies in the incapacity of the latter pair to reproduce normally under gasteromycetoid development conditions. It is not clear now whether the so-called gastroid conditions of *Suillus decipiens* (*Boletinus decipiens*, Pl. 76, 5) as described by Dodge and Singer should be taken to be another example of gastromycetation as Dodge and Singer both interpreted them, or as a gasteromycetous genus (family Gastroboletaceae). Only experimental work might - in addition to necessary further observation of this rare fungus in Florida - provide the key to the understanding of this problem.

The development of the carpophores in case of gasteromycetation is generally more or less endocarpic. We use this term for gastroid agarics and Gasteromycetes corresponding to the definition of that group in order to separate this development type from the development types accepted in Agaricales where gasteromycetation is not observed (see chapter XII). In gastroid Basidiomycetes a condition for free

spore fall and therewith spore projection by functional autobasidia is not required and has either been lost or not yet been acquired. Sporulation begins at an early stage when free spore fall is still or permanently impossible, frequently within a peridium - a situation not encountered in normally developing Agaricales.

The example of *Suillus decipiens* shows that there is a difference between gasteromycetation in the sense as the word is used here and a tendency, in the phylogenetic sense of the word, of agarics and boletes in general to run into Gasteromycetes. In other words, the term gasteromycetation, does not refer to the hypothesis which postulates a derivation of the Gasteromycetes - or some of their suborders - from the Agaricales. For a further discussion of this aspect, see chapter XXIII.

## VI. CYPHELLIZATION

Just as gasteromycetation does not imply a phylogenetic theory but the description of a phenomenon, so cyphellization as we used the word for the first time (1975), is by no means an attempt to describe an evolutionary process whereby the Cyphellaceae, whatever that is, would be derived from the Agaricales (although both Donk in Petersen 1971 and the present author (1963) believe, that some of the species formerly inserted in the Cyphelloideae or Cyphellaceae are indeed reduced agarics), but a term by which we indicate cases in which agarics loose their lamellate or poroid hymenophore. This basic characteristic of "cyphelloid" forms is mostly accompanied by several parallel developments: (1) a tendency to replace the wide extent of hymenial surface area on lamellae or pores by producing a large number of small carpophores instead of a small number of relatively larger carpophores with hymenophore, (2) a tendency to achieve such an increase in the number and reduction of size of the carpophores by doing away with the stipe - sometimes replaced by a small pseudostipe - and dense aggregation of the individual carpophores either on a stromatic body bearing them, or among an *Ozonium*-like extension of basal mycelium. The resulting fruit-body type is cyphelloid, or inverse-pezizoid.

While there is no visible advantage in the formation of gasteromycetized fruiting bodies, cyphellization is obviously a means of accelerating the life cycle under conditions which make slow carpophore formation and late sporulation hazardous because of brusk changes in the microclima or because of competition with other microorganisms. We speak of cyphellization as a process rather than of cyphelloid carpophores versus agaricoid ones because there are numerous cases where normally lamellate species either begin sporulation when the folding of the hymenial surface has not yet started, or produce at the same time larger lamellate and smaller smooth carpophores (from the same mycelium). No wonder, then, that in certain cases, the absence of lamellae cannot by itself justify the erection or recognition of a different genus. The transfer of such individuals, as would happen in the case of an artificial classification like that of Fries-Saccardo, to another family or order is not justified. On the other hand, the absence of the hymenophore and concurrent transformations in the cyphelloid fungi are undoubtedly generic characters if they are accompanied by correlated characters differentiating such cyphelloid groups from related agaricoid groups.

Cyphelloid fungi have been recognized as Agaricales in all those cases where the affinity with typically agaricoid genera was obvious, or, by a chain development, if other cyphelloid fungi could be shown to be closely related to those cyphelloids already recognized as agarics.

Cyphellization is restricted precisely to such families in which a reduction of the carpophore, particularly the stipe, appears to be within the evolutionary possibilities of the family. These possibilities are seen in such families where pleurotoid forms exist, progressing from eccentric to lateral and eventually function-less or wanting stipe. These are the families Polyporaceae, Tricholomataceae, Strophariaceae, Cortinariaceae, Crepidotaceae, Entolomataceae, Paxillaceae and Boletaceae. In some of these cyphelloid forms have not been observed. They are, however, well known and well represented in the Polyporaceae, Tricholomataceae (Pl. 64-67) and Crepidotaceae.

A discussion of the phylogeny of the cyphelloid forms belonging to the Agaricales has been published by Singer (1963).

## VII. PROTOCARPIC TUBERS

A fleshy, short-lived bulb formed before the stipe proper develops, and which is either hypogeous or epigeeous, and sometimes resembles a carpophoroid but later gives rise to one or several normal agaricoid carpophores is neither a true sclerotium nor a carpophoroid as has been pointed out by Bas (1965) who accepts, as I do, the definition of sclerotium as given by Snell & Dick (1957) whereby this is necessarily a resting body. On the other hand, by constantly germinating into a normal carpophore, this body cannot be identified with the carpophoroid. It has therefore been named protocarpic tuber by Bas. Examples of protocarpic tubers are those formed regularly as it seems in all species of *Squamanita* and *Dissoderma*. As I have mentioned before, some of the organs looking like carpophoroids in *Marasmiellus* have also been seen to give rise to normal fruiting-bodies. These individuals which do so might be termed protocarpic tubers.

The best known type of protocarpic tubers is a large bulb sharply differentiated from the base of the stipe, or a bulb-like base of the stipe which as far as known always gives rise to hyphae which produce chlamydospores. Chlamydospores have however not (yet?) been observed in the "protocarpic tubers" of *Marasmiellus*.

It is premature to discuss the nature of such stromatoid (white) formations which serve as a base for several cyphelloid carpophores, and compare them with the protocarpic tubers. One example of such common bases has been observed in a group of still insufficiently studied species of *Calypella* (Tricholomataceae). Another such example would be *Fistulina* whose position in the Agaricales is still highly controversial. In the case of *Fistulina*, the stromatic formations bearing the cyphelloid carpophores, assume the shape of a pileus and the cyphelloid carpophores are so densely aggregated that they may be interpreted as tubes of a tubular hymenophore. No wonder then, that the Fistulinaceae are still considered aphylophoraceous by most mycologists although Lohwag and Bondarzew & Singer have

repeatedly affirmed the affinity of *Fistulina* with cyphelliform Basidiomycetes (see also p. 843).

### VIII. ARTHROSPOROCARPS AND SYNDEMATOID CARPOPHORES

Bas (1965) when discussing the protocarpic tubers, compares them with *Nothoclavulina* - the clavarioid conidiocarps of *Arthrosorella ditopa*. Since the protocarpic tubers of *Squamanita* also bear an imperfect state, and since they are also the forerunner of a perfect and normal agaric carpophore, this comparison is indeed not farfetched.

The difference between the two organs consists in the nature of the imperfect fructification and the shape of the conidiocarps. While the protocarpic tubers have the shape of a tuber or bulb and bear chlamydospores, the imperfect fruiting bodies of *Arthrosorella* are shaped much like *Clavulina* and bear arthrospheres (oidia).

In this case, while it is not known what induces the production of the perfect form, possibly increased moisture, the conidiocarps do not simply "germinate" into a new, this time perfect, carpophore but they will produce a pileus on top of the clavarioid fructification which, as a whole, will serve as the stipe of the mushroom. This manner of development reminds one of the "télépodes" (p. 13) where, likewise, either humidity or light induce the formation of a pileus, with the significant difference that in the case of *Nothoclavulina-Arthrosorella* the conidiocarp-stipe is not sterile but serves as a base for the formation of arthrospheres (Singer 1950, 1970).

Arthrosphere-producing conidiocarps with clavarioid shape are called arthrosporocarps (Pl. 43). We know only a single genus which produces arthrosporocarps, and this genus is different from other genera of the Tricholomataceae not merely by the formation of arthrosporocarps but also by other characters. It is therefore assumed that the arthrosporocarp is an important character in Agaricales.

Whether the *Sclerostilbum*-form of *Collybia racemosa* is another instance of a conidiocarp of the arthrosporocarp-type, or a young stage, cannot be decided at present.

It is doubtful whether *Asterophora* ever forms completely imperfect carpophores. If it did, they would be different from both protocarpic tubers and arthrosporocarps since the chlamydospores are formed on the definitive mushroom-like carpophores which are neither bulb- nor *Clavaria*-like. But synnema- (coremium-)like chlamydospore-bearing carpophores were described by O.K. Miller in a *Pleurotus* (see also p. 70, 175, and 178).

Hilber (1982) showed that these organs have indeed taxonomic significance. They occur in and are characteristic for a section of *Pleurotus*: *Coremiopleurotus*. These carpophores are formed at the base of the stipe of the basidiocarp and occasionally in other places and have occasionally also been observed in cultures. They consist of hyphae vertically bundled and producing chamydospore-like, terminal asexual "coremiospores" which eventually become separated from the hyphae (bi-nucleate)

of the synnematoid carpophore. This conidial stage is formed by the secondary mycelium or those of the basidiocarp base. It has however also been observed to be formed by uni-nucleate hyphal cells.

## IX. STILBOIDS

In other cases, the sterile, non-basidiocarpous formations with carpophore-like appearance have a definite function as propagula, and are not at all comparable with the formations named above. This is the case with the so-called "gemmae" of *Mycena citricolor* ("*Omphalia flavidula*") which have been studied by Buller (*Res. on Fung.* 6: 387-443. 1934). Here, a sterile carpophore is formed that has a separable capitellum ("pileus") which is blown by the wind from one leaf to another and thus serves for vegetative propagation, in this case of the epiphyllous phase of the life cycle of the fungus. The "gemmae" do not form any basidia but the capitella attach themselves to the leaf by their gelatinosity and the hyphae start immediately to form new exogenous mycelium parasitic on the leaf. It is especially interesting to remember that certain species of *Mycena* - as has been shown by the anatomical studies of Kühner (1926, 1938) - have the stipe actually separate from the pileus by an intermediate zone of different structure. The carpophore-like bodies of *Mycena citricolor* were misunderstood by Cooke who described them in a genus otherwise without any relationship with the Agaricales, as *Stilbum flavidum* Cooke. The term "gemmae" used by Buller and the implication of abortion of the fruitbodies found in Maublanc & Rangel's account (*Bull. Soc. Myc. Fr.* 30: 41. 1914) are both inadequate or misleading in view of the evidence at hand, and therefore the term stilboids (Singer 1951) has been introduced to designate this specific form of propagule in Agaricales.

Other types of propagules such as the "bulbils" in the sense of Weresub & LeClair (1971) have not been found in Agaricales.

## X. BULBILLOSIS — RHACOPHYLLUS FORMS

In rare cases, the carpophore is sterile only in the sense that sporulation is suppressed, yet the function of the basidium is maintained by the formation of sclerotized short cells which form a sheet-like extension of the trama in form of lamellae devoid of a hymenium. The bodies bearing them are therefore neither carpophoroids nor stilboids, nor are they typical Agaricales-carpophores. They are called *Rhacophyllus*-forms and the phenomenon we refer to is known as bulbillosis of the agarics. The word bulbillosis in this context should not convey the notion that bulbils or even bulbil-like bodies are formed (in the sense of Weresub & LeClair, *Canadian Journ. Bot.* 49: 2203-2213. 1971). Like "gastromycetation", the term bulbillosis presumes that *Rhacophyllus* forms are aberrant fructifications of normally "mushroom"-producing agaric mycelia, especially those of the family Coprinaceae. Although the specimens I have seen show nothing but the habit to link them with such agarics, the cytology of the sclerotized cells of the lamellae

seems to be identical with that of the basidium (whereby they will then be interpreted as an extreme case of the sclerobasidium). *Rhacophyllus* forms are, in every regard, agaricoid and were therefore assumed to be Basidiomycetes.

I have collected what I believe to be the original species of *Rhacophyllus*, *R. lilacinus* Berk. & Br. in Florida which is deposited at Farlow Herbarium, but I have not obtained data from this specimen which might throw any additional light on the matter. Moreau (1913), Petch (1936), Lohwag (1936), Reijnders & Malençon (1969) have stressed the agaricoid features of these fungi in anatomical, cytological, and developmental investigations, evaluating the morphology of *Rhacophyllus*.

Maniotis (1964) undoubtedly has provided the most enlightening data particularly on the connection, now experimentally demonstrated, between *R. lilacinus* and a *Coprinus* he called *C. clastophyllus*. Reijnders & Malençon (1969) provided data on the individual development of the *Rhacophyllus*-form. They found that opposite sides of lamellae join to form series of "bulbils" situated where we normally find the interlamellar spaces.

It is true, no successful attempts to link *Rhacophyllus*-forms to existing species have been published earlier. There are no published field observations which would permit to accept any of the known *Rhacophyllus*-forms as merely a state or aberration of normal *Psathyrella* carpophores. My own interpretation of *Amparoina* as an agaric which in a later state of development becomes a *Rhacophyllus*-form was incorrect since *Amparoina* is an agaric near *Mycena* which (as in the type) tends to form early-sporulating forms (gasteromycetation).

Under these circumstances, there can be no doubt that the production of true *Rhacophyllus* forms instead of normal agaric carpophores represents a character of taxonomic interest and it would seem that such forms occur only in one family of the Agaricales, the Coprinaceae.

## XI. DEVELOPMENT OF THE PRIMORDIUM OF THE CARPOPHORE

by A.F.M. Reijnders

The rapid progress of biochemistry and the use of the electron microscope have caused the development of morphogenetic methods to become, to a certain degree, separated from earlier data which have been obtained by light microscopy. Nevertheless, it might be harmful to treat the observations obtained by both these methods separately or to neglect completely the facts revealed by what at present is often called developmental morphology (Taber in Ainsworth & Sussman, "*The Fungi II*" 1966: 387). Since light microscopy and electron microscopy are complementary to each other in many cases (e.gr. in the analysis of the structure of the spore walls, see Kühner 1980: 29), the structural characteristics which can be observed by light microscopy can provide useful information for the EM researcher. Essentially, we are dealing with different aspects of the same entity inasmuch as fine structures underlie larger complexes. In many instances the latter will indicate where submicroscopical research can be fruitful. Biochemical analysis of the processes

during the elongation of the stipe under various conditions has been carried out very thoroughly, including work on etiolated stipes grown in darkness. The simple microscopical observation of such stipes can tell us which etiolation is the consequence of cell division in the upper zones and which part must be attributed to cell inflation below the dividing zone.

The number of submicroscopic investigations concerning cells of the carpophores of Agaricales is increasing rapidly. Yet, they concern mainly the hymenial cells (Wells & Wells 1982). Considerably less is known about the somatic cells in this respect. Nevertheless, there are a few very thorough studies at hand and we need only to compare Wessel's results on *Schizophyllum commune* and those by Moore et al. on *Coprinus cinereus* (Schaeff. ex Fr.) S.F. Gray to conclude that submicroscopic features will be of paramount importance to taxonomy in the future. Gooday (in Wells & Wells l.c.) remarks that "the study of morphogenesis of the agaric fruit body can provide a model system for the elucidation of the *controls of differentiation* in multicellular eucaryotes". In *Schizophyllum* (which is not an agaric but rather belongs in the Aphylophorales) and in *Coprinus cinereus*, a true agaric, the differences between metabolic processes which are morphogenetically significant, are striking. The storage of reserve material is different because the carbohydrates in *Schizophyllum* are stored as R-glucans in the thickened cell walls whereas in *Coprinus cinereus* important reserves of glycogen are deposited in the basal plectenchyma, the lowest part of the primordium, representing a tissue not belonging to the stipe. The formation of the pileus in *Schizophyllum* depends, as Wessels established, upon a low but continuous supply of glucose which derives from cell wall degradation in other primordia and in the stroma. Anatomically, there is no evidence for such a separate position of the pileus. Since *Schizophyllum* represents a type characterized by diffuse development (Reijnders 1963) there are no striking anatomical differences between the tissue of the pileus and that of the primordial shaft. In *Coprinus*, the pileus is quite another thing; it is present almost from the very beginning of primordial development. The development of *Coprinus cinereus* is therefore called pileostipiticarpous. Moore et al. emphasize the different metabolic processes in pileus- and stipe-tissue of *Coprinus* (see below). But biochemical and submicroscopical data will not be important only for the comparison of taxonomically distant groups. Submicroscopic differences exist also on the species level. They might become important for the evaluation of taxa, as has been shown by Eymé & Couvy (1974) for *Agaricus sylvicola* and *A. bisporus*. This concerns peculiar fibrillary, organized bodies which are present in mycelial strands and young primordia of *A. sylvicola* but are absent in the corresponding tissues of *A. bisporus* although the authors found in one special strain of the latter some intertwined microfibrillae of proteinic nature which, however, did not reach the complexity in structure observable in *A. sylvicola*. Though the two species belong to different sections of the genus *Agaricus*, these examples show that ultrastructural facts may become increasingly important at every level of taxonomic mycology in the future.

However, biochemical and ultrastructural research on cell differentiation in Agaricales and other groups of macromycetes is only in an early stage of its

development.\* Consequently, we have to confine our observations to the facts which have become available and evident through the study of "developmental morphology" (in a more restricted sense) and detectable by light microscopy. Even in this respect there are many hiatuses and the number of species with well known ontogeny is still too small. It will not be necessary to examine all species - if this were possible - because there are certain conformities and rules concerning whole groups (see below). If this were not so there would be no relevance for the systematist. But it is still insufficiently known just how these structures are allocated. Although veils in mature carpophores are only remnants of primordial structures and can therefore be more completely studied in the primordium, it is possible to determine their presence or absence in all species of a monographically studied group: yet, their real nature and origin often remains obscure, especially where we have weak structures. Scattered remnants of the veil above the pileipellis (epicutis) are often taken for hyphae of the latter itself (Reijnders 1979: 410) because their origin is not taken into account. Furthermore, the limits of primordial structures are often insufficiently known when a large series of species is compared and relationships should be evaluated. Thus, in many cases, the application of ontogenetic criteria in taxonomy remains provisional and lacking in forcefulness (probably too much so).

The question of angiocarpny has always been the most discussed subject in the field of ontogenetic structures of the carpophore. The latter must be called gymnocarpous when the rudiment of the hymenium is not covered by any layer and when the margin of the pileus is not pressed against the stipe for a long time (pl. 85 fig. 1). It was mainly Patouillard who emphasized these characteristics by assuming that Gasteromycetes were angiocarpous (the hymenium arising inside other tissues); that the Agaricales were hemiangiocarpous (the hymenium arising internally but during further growth of the carpophores being set free by a tearing-up of the outermost tissue layers - the veil); and that the Aphylophorales were gymnocarpous. At present, this distinction has lost much of its value. As has already been shown by research done by Atkinson and his pupils, by Kühner and others, it is not true that all or even a large majority of the Agaricales are hemiangiocarpous. Many of them are gymnocarpous. It is not even true that all Gasteromycetes are angiocarpous in the sense of the definition given. For those who consider the Gasteromycetes a heterogeneous group, a common characterization makes no sense and for those who do not, the functional characteristics of the basidium and the lack of a spore print will prominently enter the definition. In the Agaricales, angiocarpny is present when the rudiment of the hymenophore or the area where it will come into being is first covered by a layer or by the margin of the pileus so that it is not exposed. Recent analysis of the primordia of many species has shown that angiocarpny is a term covering various structures which can be very distinct but may also be extremely ephemeral. Thus, it will be impossible to determine, in a large number of cases, the kind of angiocarpny by observation of the carpophores under exclusion of the primordia.

The distinction between primary and secondary angiocarpny is the most striking feature relative to the understanding of these variations because the types of angi-

\*The book by Moore & al. (1985) which came to my attention when the present chapter was in proof, deals with morphogenesis in Agaricales from all angles.

carpy are the consequence of different processes. The development of the covering of the hymenophoral rudiment in which the cover results from an outgrowth of hyphae emanating from a preexistent part of the primordium, e.gr. the pileus-margin or the stipe or both, has been called secondary angiocarpy. If the outgrowth derives from the margin of the pileus, we are speaking of a *pilangiocarpous* form (pl. 85 fig. 2), if from the stipe, the primordium is stipiticarpous (pl. 85 fig. 3), and it is called *mixangiocarpous* (pl. 85, fig. 4) when the hyphae emanating from the surface of the stipe merge into hyphae which have grown out of the surface of the pileus. In all three cases these outgrowths bring about a seclusion of the young hymenophore.

All these possibilities are rather frequent in the Agaricales. The pilangiocarpy is particularly common in those cases where the margin of the pileus is pressed against the stipe during a rather long period of the development with or without a conspicuous widening. In this case the primordium is often looked upon as gymnocarpous because the enclosure of the hymenium is often maintained only in minute primordia.

When secondary angiocarpy was discovered (Kühner 1925, 1926) it was called pseudoangiocarpy. This term can hardly be maintained in view of the frequency of metavelangiocarpy which will be explained below after we have dealt with primary angiocarpy.

Primary angiocarpy is caused by quite a different principle, viz. the internal origin of the elements of the hymenophoral rudiment. At first, there is often a primordium formed which consists of entangled hyphae. These are generative hyphae directed sometimes more or less longitudinally. This can be very troublesome for the observer when he attempts to determine the beginning of the formation of the stipe (see below). But the totality of the undifferentiated hyphae (which we call protenchyma) gives locally rise to lateral branches which are directed outward and downward and which constitute the rudiment of the hymenophore. If they do not arise at the periphery but at a more or less distinct inward position, they appear covered by already pre-existing hyphae, sometimes only a few, but they form also frequently a hymenophoral ring perpendicular to the axis of the primordium, situated more towards the interior of the primordium.

The variations of this primary angiocarpy are determined by the formation of the veils. If the hyphae at the periphery of the primordium remain unchanged (i.e. protenchymatic) some undifferentiated tissue can remain between the hymenophore and the upper part of the stipe-surface which is located somewhat more inward. The pileus-margin arises outside the hymenophore-rudiment and is characterized by a fascicle of parallel hyphae, which are directed downward and at first often inward. The tissue below this zone is often very ephemeral and therefore unobserved when the carpophore has matured but it can also develop into a voluminous organ (the annulus or ring) by intercalary growth and hyphae which emanate from the stipe. We call this tissue "lipsanenchyma" and not partial veil (see below). This mode of angiocarpy has been called *paravelangiocarpy* (pl. 85, fig. 5) and can be present when the origin of the hymenophore is to be found near the surface or covered by a wide lateral part of the pileus. It sometimes occurs that no tissue has been left between pileus and stipe-surface but that the internal hymenophore is set free by the tearing

up of the protenchymatic hyphae at the outside only: in this case the paravelangiocarpous mode merges into the *gymnangiocarpous* mode (pl. 85, fig. 6), without any trace of a veil afterwards.

When in young stages there is a particular differentiation of the outermost tissue of the primordium and in most cases it concerns the whole surface, we speak of a universal veil which in consequence also covers the hymenophore-rudiment. Sometimes this envelopment represents only a slight alteration of the protenchymatic hyphae, in other cases it develops into a striking structure the remnants of which are frequently used for taxonomic purposes (volva, patches on stem and cap, hairy coatings, cortina, the margin of the ring, etc.). During this prolonged phase of growth the universal veil is often reinforced by hyphae which emanate from stipe- and pileus surfaces, and this is the principle of secondary angiocarpy. When these two modes, which are generally combined, are in the beginning more or less separated, we speak of *metavelangiocarpic* development (pl. 85, fig. 9). This is e.g. manifest when the universal veil or its remnants are pushed outward by a renewed outgrowth of hyphae at the periphery, so that the original primary universal veil (innate veil) becomes less voluminous than the emanated veil. Since metavelangiocarpy - not uncommon in Agaricales - is composed both of primary and secondary angiocarpy, the term *pseudoangiocarpy* does not fit well in our scheme of terms. A primordium or a species cannot be both angiocarpous and *pseudoangiocarpous* (i.e. seemingly angiocarpous). Thus it is preferable to avoid a possible contradiction in terms and we do not use the term *pseudoangiocarpous* any more.

Many cases are known where a more or less conspicuous universal veil is differentiated in absence of any lipsanenchyma. Such primordia have been named *monovelangiocarpic* (pl. 85, fig. 7). When universal veil and lipsanenchyma are both present, we are speaking of a *bivelangiocarpic* form (pl. 85, fig. 8). When the lipsanenchyma is scanty we do not observe it when the carpophore is adult but often it participates in the formation of a visible ring. This latter organ can thus be composed of lipsanenchyma only, of the universal veil only or of both. In all these cases the remnants of these primordial structures are called "partial veil" in descriptions of mature carpophores; therefore we abandoned this form for the sake of greater correctness. We recommend the use of the term lipsanenchyma, also in mature mushrooms when it is outlined clearly against the universal veil (the outer border of the ring).

To resume:

1. The hymenophore-rudiment is enveloped by secondary outgrowth of hyphae:  
**secondary angiocarpy**
  - a) The outgrowth comes out of the stipe: *stipitangiocarpy* (pl. 85, fig. 3)
  - b) The outgrowth comes out of the pileus: *pilangiocarpy* (pl. 85, fig. 2)
  - c) The outgrowth comes out of both: *mixangiocarpy* (pl. 85, fig. 4)
2. The hymenophore-rudiment is enveloped by preexisting hyphae (a part of the original protenchyma):  
**primary angiocarpy**
  - a) There is a universal veil but no lipsanenchyma:  
*monovelangiocarpy* (pl. 85, fig. 7)

- b) They are both present: *bivelangiocarp* (pl. 85, fig. 8)
- c) There is only a lipsanenchyma but no universal veil: *paravelangiocarp* (pl. 85, fig. 5)
- d) There is no trace of a veil, also in small primordia: *gymangiocarp* (pl. 85, fig. 6)

The hymenophoral trama develops further normally by hyphae, completing it, growing downwards. One can speak moreover of bulbangiocarp when the universal veil is differentiated at the periphery of a primordial bulb (*Volvariella*). This is mostly a special case of bivelangiocarp.

The universal veil as well as the lipsanenchyma can remain scanty or without well defined differentiation, but both can develop into a mighty organ (*Amanita*) and these various structures are important in taxonomy.

A second topic of developmental anatomy is the succession of the parts: stipe, pileus and hymenophore. This was emphasized for the first time by Atkinson and his pupils. It has become apparent that the differences in succession are correlated with the external shape of the primordium. This peculiarity is probably even more important for taxonomic evaluation than angiocarp but, though it is expressed very clearly in extreme cases, it is often very difficult to define. The difficulty consists in the precise determination of the characteristic indicating the beginning of the development of each part. The structures which have been considered in this respect are the product of complicated morphogenetic processes. Most clearly visible and nearly always constant in the beginning is the construction of the hymenophore, perceptible by ramifying of hyphae situated somewhat inside the pileus-margin in the upper part of the primordium, these branches will be directed downward. The outset of the pileus-formation can be detected by the formation of a fascicle of parallel hyphae at the outside of the primordium, which is directed outward and downward. But there is reason to suppose that in many cases pileus-differentiation has begun before the presence of such a bundle. It is possible that in a primordium, consisting of a homogeneous plectenchyma, the difference between the upper part, where the pileus will arise, and the lower part which is destined to form the stipe has begun long before it is perceptible by light-microscopy, leaving the basal plectenchyma out of consideration. A dense mass of stain-absorbing ramifying hyphae marks these zones in many genera, therefore they are often visible in colored sections. It is most difficult to define the beginning of stipe-formation. In plectenchymatous primordia this is often preceded by hyphae which assume a longitudinal direction and will constitute a meristemoid. Unfortunately this is not always a reliable mark: The longitudinal direction is sometimes present in the protenchyma from the earliest beginning of the primordium; moreover, this characteristic is somewhat influenced by the length of the maturing stipe. The beginning of cell-inflation in these parallel hyphae is probably a somewhat better criterion.

In their important study of the relations between metabolic processes and morphogenesis in *Coprinus cinereus* Moore et al. (1979, l.c.) have much emphasized the local differences in biochemical evolution of pileus and stipe. We quote: "The glycogen is utilized in the cap and the consequent great increases in glycolytic inter-

mediates creates the conditions whereby many metabolic systems can be regulated by catabolite concentration".

Osmoregulation occurs in cap and stipe "but in the former nitrogenous metabolites predominate, while in the latter simple sugars are formed as osmoregulatory materials" (l.c.: 715). So it may be expected that in the future these basic processes will enable us to define more accurately the intraprimordial relations which are only partly visible by light-microscopy.

Nevertheless, when we compare the slender, elongating primordia of many Agaricales with the short, thick-set form of others remaining so for a long time, the differences are so striking that we must pay attention to them, inasmuch as it turned out that many taxa behave in the same manner in this respect. (Reijnders 1974 Pl. 2, 1979 Pl. 1, fig. 1, Pl. 2, fig. 11, 12, etc.). Consequently, there is a *concentrated type* of development with short and thick primordia, remaining so for a long time, and, what we called a *diffuse type*, where the hyphae are more or less parallel from the beginning and where the pileus arises by fan-like spreading of these hyphae. All intermediates exist. We think that the diffuse type is more primitive. The process of concentration consists of a shortening (at least in the first phases) of the branches of the generative hyphae and of an anticipation of the differentiation. It has to do with the strong inflation of the cells which is very important for the extension of the carpophore in many genera (*Coprinus*, *Conocybe*, etc.) although not all species with strong hyphal inflation have a concentrated development.

With a view to all reserves we dealt with just now, our scheme of types of concentration is rather detailed: all these types (Pl. 86) may present themselves or become merged.

- a. The very young carpophore is composed of a fascicle of parallel hyphae, not topped by a plectenchyma (fig. 1): *stipitocarpous*
- b. There is at first a primary protenchyma composed generally of interlaced hyphae: the intercalary growth of the center of the protenchyma in the upper part or the formation of the parallel hyphae of the pileus-margin begins independently of the stipe but they don't show up clearly before the longitudinal hyphae of the stipe become distinct. The plectenchyma of the cap-center is not formed by the stipe (fig. 2): *Pileostipitocarpous*
- c. The intercalary growth in the center of the primordial plectenchyma or the development of the margin of the pileus or both are distinctly visible before the longitudinal stipe-hyphae appears (fig. 3-4): *pileocarpous*
- d. At the moment of the appearance of the palisadic hyphae of the hymenophore, one observes the first indication of pileus-development (margin of pileus or very distinct intercalary growth) of the hyphae of the stipe (fig. 5): *isocarpous*
- e. At the moment of the appearance of the palisadic hyphae of the hymenophore, one observes also the first indication of pileus-development (generally the parallel hyphae of the margin) but the differentiation of the stipe becomes obvious later: *hymenopileocarpous*

- f. The palisadic hyphae of the hymenophore rise in a circular zone in a primordium which is entirely composed of primary protenchyma and not differentiated (if we disregard veil and cortical layers) (fig. 6): *hymenocarpous*

Another structural difference occurring only in primordia which is undoubtedly of taxonomic interest is the way in which the lamellae arise in some genera. The inception of the hymenophore is generally marked by ramification of the hyphae in an annular zone, perpendicular to the axis of the primordium in its upper part. These lateral branches are directed downward and form a palisade. Somewhat later hyphae along radiating ridges grow down, pushing the palisade-hyphae downward or sideways, to constitute the hymenophoral trama. This common way of gill-formation by folding of a pre-existing plane of palisade-hyphae is called the *levhymenial* mode. (Pl. 86, fig. 7). There are only two exceptions: the *rupthymenial* and the *schizophytenial* way of gill-formation. In both cases there will never be a coherent plane of palisade-hyphae at the beginning. In the first instance the palisade-hyphae arrange themselves along radiating lines alternating with strips where the original protenchymatic hyphae remain, connecting the pileus-trama with the tissue underneath the hymenophore. (Pl. 86, fig. 9). Very soon the radiating sectors with the palisades become arched downward. The hymenophoral trama develops further in a normal way by hyphae which complete it, growing downward. All intermediates between this manner of hymenophore-formation and the levhymenial one can be observed. It is to be found in genera with highly concentrated primordia: *Coprinus* (Reijnders 1979), *Psathyrella*, *Panaeolus*, *Conocybe*, and *Bolbitius*. In the *schizophytenial* mode the hymenial-palisade arises at the side of vertically oriented sheets, separated by narrow fissures; the trama-hyphae are parallel and vertical and connect the pileus-trama with the lipsanenchyma. This mode has been found only in *Amanita*, no intermediate structures are known. (Pl. 85, fig. 10).

In this book some remarks must be made on the relevancy of these ontogenetic data to systematics. In the beginning of this century several investigators had great expectations as to the taxonomic value of ontogenetic structures. Probably they thought it possible to trace in this way fundamental structures like e.g. the bronchial arches and their phylogenetic evolution in animals. When we survey the whole of ontogenetic structures in Gasteromycetes and Agaricales we will not deny that some indications of phylogenetic metamorphosis, which will not be dealt with here, are recognizable, but in general we have to do here with mobile and mutable features, which may be constant on the species-level but which are considered to represent structures with a great adaptive power, even with respect to primary angiocarpny. A recent investigation into the ontogeny of *Tectella* corroborates this conclusion in an unexpected way (Reijnders 1983): *Tectella*, a genus closely related to *Panellus*, shows a deep primary angiocarpny and the palisade-layer of the hymenophore is formed at a very early stage. Nevertheless somewhat later the primordium (cup-shaped) develops in a non-concentrated way with strongly outgrowing parts and the cell-inflation is in this species not very important. On the other hand the constancy of ontogenetic structures in many genera, even in tribuses, is striking; we shall give below some instances. Thus these characteristics are comparable to those expressed

by "gross morphology", to which formerly a greater taxonomic value was imputed, e.gr. the configuration of the hymenophore, decurrent lamellae, a cup-shaped or a bulbous shape, etc. We think their importance for taxonomy is also equivalent to that of amyloidity of tissues, of clamp-connections, etc. We have to take into consideration that both angiocarpny and succession of the parts are the result of intermingled but different processes, which can have a different value for taxonomic purposes. We have pointed out therefore that there are three processes which influence veil-formation: 1. differentiation of the parts not at the periphery of the primordium but deeper inward, 2. outgrowth of hyphae, 3. metamorphosis and development afterwards (spherocyst-formation, gelatinizing, ramification, etc.). We dealt already with the different processes which may affect the succession of the parts (various metabolic aspects, ramification of hyphae, forming of meristemoids, etc.). One of the possibilities to estimate the evolutionary trend which has given rise to the various types of succession may be expressed by the following order: stipitocarpous, pileostipitocarpous, isocarpous, hymenopileocarpous, hymenocarpous, pileocarpous. In diffuse types of development which are stipitocarpous, the hymenophore is the element formed last. When the palisade of the hymenophore arises before we see differentiations which are proper to stipe or pileus, it may represent the strongest anticipation.

We think that two groups with somewhat different conduct i.e. 1. species with a strong inflation which develop in a short time and 2. many micorrhiza-formers like *Amanita* are characterized by a pronounced concentrated development. It is not possible to deal here with the results of ontogenetic investigation in detail (see the genera). Only some striking features will be mentioned in addition to this survey. Reijnders has recently tried to collect new data to complete those already known (1975 Agaricaceae, 1979 Cortinariaceae, 1979 Coprinus, 1983 Tricholomataceae) whereby it could be established that the new facts fit generally well with the developmental pattern of the examined group. The Tricholomataceae, an extensive family, will never reach a strong concentration, but some species are somewhat isocarpous. In most cases they are stipitocarpous. The angiocarpny ranges from gymnocarpny to bivelangiocarpny: striking is the constancy of the paravelangiocarpny in *Marasmius*, *Marasmiellus* and *Micromphale*. The Amanitas are homogeneous: bivelangiocarpous, pileocarpous and schizophyrial, but the species of *Limacella* are less specialized. In the Pluteaceae we meet with the very peculiar bulbangiocarpny, coupled with the appearance of the cap in a cavity in *Volvariella*, but in the probably concentrated primordia of *Pluteus* the facts about angiocarpny are insufficiently known for it is difficult to obtain a set of young primordia. In the family of the Agaricaceae there is much variation. In *Agaricus* the primordia are generally highly concentrated and bivelangiocarpous, in *Lepiota* they are less concentrated. In the Coprinaceae there is also rather much variation as to angiocarpny and the concentration (at least pileostipitocarpous). Striking is the hymenocarpny and the paravelangiocarpny (or gymnangiocarpny) in all Bolbitiaceae and in *Panaeolus*. Kühner has remarked that this combination is frequent in genera with a hymenoderm. The lack of a universal veil in such primordia might often be result of reduction of this organ. In the family Strophariaceae there are no stipito-

carpous species, the angiocarp ranges from mono- to bivelangiocarp. In the family Cortinariaceae velangiocarp occurs as a rule, often it is monovelangiocarp (*Inocybe*), bivelangiocarp is more exceptional. Thus the cortina forms part of the universal veil, as do the fibrous remnants on the stipe (*Cortinarius*). The more the species have a bulbous stem the more the primordia have a concentrated development: in *Phlegmacium* there is a pronounced pileocarp, also in *Leucocortinarius* but the taxonomic position of this genus is contested. But there are also many stipitocarpous species in this colossal family (*Telamonia* etc.). The Entolomataceae have been the subject of only a few ontogenetic investigations but it seems that gymnocarp and stipitocarp are basic here. With respect to the boletoid families (Paxillaceae - Strobilomycetaceae) it must be concluded that when the hymenophore is covered in young stages, this is often a secondary angiocarp, though all species of *Gomphidius* are metavelangiocarpous, the latter mode occurs also in *Gyroporus* and *Strobilomyces*, a temperate primary angiocarp thus being possible here. Many species are stipitocarpous, others are pileostipitocarpous. Many species of *Boletus* with their bulbous, globular primordia must possibly be looked upon as having a very concentrated development, though they are generally gymnocarpous. The same consideration will hold good for *Russula*, with primordia, which remain subterranean for a long time and which are mostly wider than high. But *Lactarius* has often slender primordia: stipitocarpous. There is certainly need for more ontogenetic data in these genera, as in many others.

## XII. THE VEIL

by A.F.M. Reijnders

Ontogenetic analysis has shown that veil formation is the result of three rather independent processes (see also the chapter on development of the primordium):

1. An envelope (consisting of generative hyphae or protenchyma) is saved at the outside of the primordium by the differentiation of the hymenophore or the margin of the pileus or the cortex of the stipe, which are situated further inward. This is the *innate* veil, which often envelops the whole primordium but may manifest itself also locally (underneath the pileus-margin). Sometimes the outermost layer of the primordial bulb is differentiated into an innate veil.
2. The veil may arise from hyphae which grow outward from a surface or a structure which is already present: this is the *emanated* veil. In this case the emanated veil may cover the whole primordium; but mostly it is present only underneath the pileus-margin and then it is formed by hyphae arising from this structure or from the surface of the stem.
3. The innate or the emanated veil may be further transformed. As for the former, it is mostly strengthened during further development by a multitude of hyphae coming out of less superficial layers: so it is necessary to observe the origin of the veils in very young stages to determine their nature. Veils may also develop further by intercalary growth. Some types of transformation are very common and manifest

themselves in various sections of the system of Agaricales, e.g. the spherocyte-veil, consisting of chains of spherocytes (*Amanita*, *Coprinus*, etc.), the gelatinizing veil (*Stropharia*, *Myxarium*, *Gomphidius*, etc.) the veil with Rameales-structure (*Marasmiellus*, *Coprinus* sect. *Alachuani*).

Veils are organs of the primordia: they reach their largest extent in the primordial stage. Many particular structures during this period suggest that they have a protective function in the young primordium, protecting especially the portion where the hymenophore develops. Sometimes the universal veil is not coherent but instead of this we find a cover of dispersed hairs: When hairs with a specialized structure are present round the young carpophore, on the cap as well as on the stem, we may consider these as a transformed veil and in such cases it is often difficult to establish the nature of the veil: innate or emanated (*Coprinus auricomus*, species of *Mycena*).

As veils function exclusively in juvenile stages, in mature carpophores we meet only with their remnants which, as Lohwag has pointed out, have lost their protective function. These remnants manifest themselves generally with a certain constancy, not only with respect to the location but also structurally and consequently have often been used in taxonomy. There have been many attempts in favor of an adequate terminology of these structures which are sometimes conspicuous but which in other cases may easily be overlooked (Gilbert 1947). Fries distinguished a *universal* and a *partial* veil. The first designation is still quite relevant but it is better to avoid the term partial veil or to use it in a very limited sense, only on behalf of the description of mature carpophores. The ring-like organ round the upper part of the stem (annulus) may be composed of various structures: lipsanenchyma (protenchyma left between pileus-margin and stem); universal veil; lipsanenchyma + universal veil; emanated veils, etc.

It might be useful to denominate some striking types of veils in behalf of the description of mature carpophores:

1. The *volva* is a general enveloping layer (universal veil) in the egg stage of the carpophores. In the Agaricales it is membranous and mostly firm. This kind of envelope has been observed in several not related genera. It remains mostly more or less distinct in adult carpophores as a cup or concentric belts or scales at the base of the stipe and/or as coarse warts or volvapatches on the surface of the pileus. Parts of double annuli (*Catathelasma*, some species of *Agaricus*, probably also *Rozites*), may locally be considered as a special form of volva (universal veil) where on the lower part of the stipe the volva is appressed or reduced to an innate covering. In such cases the annuliform i.e. ring-like portion of the volva may be referred to as an "annular volva", cf. below "annulus inferus".

2. The *pellicular* veil and the *cortina*. These are remnants of a universal veil and are later ruptured by the expansion of the pileus and/or the stem whereby they are extended and thinned. If this layer is gelatinized, this kind of veil is called *pellicular veil*, a term originally introduced in the specific case of astipitate carpophores. If it is dry and arachnoid it is, since Friesian times, called *cortina*. Both pellicular veil and cortina and of course also the volva are essentially the products of velangio-

carpous development (primary angiocarp) and should not be applied unless it is reasonably clear that the organ referred to belongs to a species with velangiocarpous development.

3. The *marginal veil*. This type of veil formation is due to the incurving margin, which comes into contact with the surface of the stem. In many cases there are hyphae which grow out from the pileus-margin (pilangiocarp), in others there is a bundle of hyphae coming from the stipe-surface (stipitangiocarp) or there are two bundles which meet each other and entangle (mixangiocarp). Later, when the pileus expands, the separation may not take place exactly at the plane of the original contact. In this case, but also when there is a pellicular veil or a cortina, remnants of the veil may adhere at the pileus-margin (velar appendiculation of the margin) or to the apex of the stipe or slide down from the apical to the central or basal portion of the stipe (annulus of the stipe). This annulus is sometimes an annulus mobilis, but the annulus mobilis of *Macrolepiota procera* is not a remainder of a marginal veil but originates from a local thickening of the universal veil.

4. In descriptions of mature carpophores the term: "annulus superus" is of common use to designate a large pending ring or according to the definition of many authors: a ring which is torn off and separates from the stem in an upward direction. Mostly this ring (it is present in *Amanita*, *Agaricus*, etc.) consists of a voluminous lipsanenchyma, which has expanded by intercalary growth or by hyphae which have emanated from the pileus margin and from the stem surface. Only in a few cases it has been observed that the edges of the young gills open to allow the passage of the hyphae toward the lipsanenchyma which is strengthened by this phenomenon (*Agrocybe aegerita*, but not *Amanita*). Only when this happens there might be a reason to speak of a hymenophoral contribution to the formation of the "partial veil", but a veil which has exclusively a hymenophoral origin does probably not exist in Agaricales. The edge of the ring is mostly formed by the universal veil and shows often the color of the latter structure. Sometimes there are remnants of the universal veil under the pendulous ring as well. An "annulus inferus" is a ring-like structure, generally fixed to the stipe underneath the free edge. Rather complicated structures may result from the simultaneous expansion of pileus-margin, veil and stipe during development of the young carpophore, viz. double and triple rings, etc. The ontogeny of such structures has already been elucidated by Atkinson (see also Reijnders 1963: 290-1). Romagnesi (1977) has pleaded in favor of the taxonomic value of such structures on a larger scale in *Agaricus*.

Lohwag (1926) supposed that the ring of *Amanita* (Lohwag's "Manschette") has hymenophoral origin, perhaps mainly in view of the spherocytes which are abundant in the veil of this genus. In this respect he admitted the homology of such organs as the receptaculum and the indusium of the Phallineae with the veil of *Amanita*. But the spherocytes or inflated clubshaped elements in the whole trama of *Amanita* are swollen tips of lateral branches of the hyphae; this typical *Amanita*-structure occurs also in the veil and is not necessarily homologous to the pseudoparenchyma of the receptaculum of the Phallineae. Moreover, as we stated above, there are no hyphae which grow from the hymenophore into the veil (that is to say in the examined species of *Amanita*).

The veil in the widest sense, i.e. the involucrum in Persoon's terminology, has been considered as being of the utmost importance in taxonomy as far as Fries and his school were concerned and an disproportionate overemphasis was put on it in such classifications as those proposed by Karsten, Schröter and especially Earle. This was partly understandable since the veil was considered the first step toward the higher forms or rather a criterion of higher forms as such. More recent analysis of veil-formation has brought to light that it is due to different processes: the taxonomic value of emanated veils (which apparently may arise in a relatively short time during evolution) must be considerably smaller than the presence of innate veils or their remnants. Nevertheless, the importance of the latter has likewise been overestimated in systematics. The complicated relations of the veils should be considered separately for each genus or tribus, particularly in view of the metamorphoses of their hyphae.

These restrictions do not alter the fact that presence or absence of veil-fragments are continually used for the purpose of delimitation of systematic groups. By doing so one should be aware of the fact that in many cases structures of the veil are mistaken for those of the pileipellis. The unknown transformations of the elements of the universal veil and the fact that the construction of the veil over the cap differs sometimes slightly from that seen along the surface of the stipe promote such misinterpretations (Reijnders 1979: 409, *Coprinus*, etc.). Many velar formations are still puzzling, even if some ontogenetic hypothesis is temporarily admitted. We do not know exactly what to think of the annulus of *Chamaeota* and many other genera.

The rather great number of factors which determine the final structure of veil-remnants make it understandable that in some cases very natural groups such as *Suillus* among the Boletaceae and *Russula* and *Lactarius* among the Russulaceae contain species with well-developed marginal veil and some without any veil and the veiled forms are often more closely related to evelate forms than to other veiled forms. This is why the emanated veil has become a hereditary structure in a short time during the evolutionary history of fungi and may manifest itself where it is needed. In *Amanita* forms with a conspicuous annulus occur together with exannulate species (*Amanita fulva*, *A. gemmata*) but Atkinson showed that in the last case the lipsanenchyma is present as well, but adheres to the stem: its separation from the stem is the only difference. On the other hand, closely allied species are distinguished in the genus *Gymnopilus* almost exclusively by the presence or absence of the cortina and the degree of its development. In such cases the absence of the veil on mature carpophores is not an indication of its absence in a primordial stage since many veils do not develop further and are pushed off long before maturity. In a fairly large number of genera the veil is used for the delimitation of sections (*Coprinus*, *Pholiotina*, *Agrocybe*). In *Amanita* again the consistence of the volva (membraneous or friable) is important for the delimitation of sections.

### XIII. STRUCTURE OF THE CONTEXT OF THE CARPOPHORE

Research on the anatomy of the context of the carpophore has been called "hyphal analysis" by Corner. Until then, in the Agaricales, there was merely a distinction between the "fundamental tissue" and the "connective tissue" as named and described by Fayod (1889) and interpreted by subsequent authors. As a basic and rough differentiation, this distinction may still be acceptable, if we define the elements making up the fundamental tissue, and add as a third category - the conducting system and its elements.

The elements of the "fundamental tissue" are, in our interpretation (1) the inflated multiseptate hyphae with firmer walls - generally the mature hyphae formed early in the development of the carpophore, as contrasted with the more actively growing thin and thinwalled hyphae of the connecting tissue, (2) the sclerified hyphae of Donk (1964) which are a thick-walled variation of the generative hyphae, (3) skeletal hyphae (Corner 1932 and later), (4), the fusiform-skeletal hyphae (Corner 1966) which, it appears to us, differ from type (1) mainly in being long, fusiform, and thus "taking the place of the skeletal hyphae in the usual dimitic construction" (Corner 1966, see also below), (5) the ligative or binding hyphae (Corner 1932 and later), (6) the spherocyst nests of the heteromerous trama (see below).

The elements of the connective tissue consist of the generative hyphae and the tendril hyphae ("hyphes sarmenteuses", "interweaving hyphae") as defined and illustrated by Corner (1950) and more clearly by Maas Geesteranus (1967).

The basic differentiation, emphasized by Fayod, can and should be developed in further detail.

In the first place, there are among the Agaricales and particularly among those with reduced morphology (cyphelloid forms) many taxa which may be characterized by the presence of only one single type of hyphae.

Secondly, as early as 1923, those tramas which consist exclusively of hyphae (whatever their characteristics) have been called homoiomerous (Beck v. Managetta, Singer 1939) in contrast to those tramas which consist of "nests" of spherocysts (Pl. 29) generative hyphae and which have been termed heteromerous. The terms "homoiomerous" and "heteromerous" are also used in lichenology in a broader sense yet they have a similar meaning. Corner (1966 p. 176) has used the term, in my opinion arbitrarily, for a structure where long, voluminous, unbranched hyphal cells with often thickened walls accompany the ordinary generative hyphae in the genus *Troglia sensu lato* (Corner). The use of the term "heteromerous" in this new sense is confusing. A heteromerous trama is one in which nests of spherocysts give the trama a rigid-fleshy consistency. In the Agarics it occurs but in a single family: Russulaceae.

While the homoiomerous trama (even if it is far from being homogeneous) consists exclusively of hyphae (whatever their characteristics), the heteromerous trama with its nests of spherocysts (called spherocytes by some, pl. 29) and accompanying generative hyphae has been studied since Corda (1839) illustrated the rosettes of

spherocysts with their axillar hypha (cp. Reijnders 1976). Through Reijnders's work it has become evident that this axillar hypha present in the center of all simple rose-knots (e.g. in the stipe of *Lactarius*) must induce the spherocyst-formation, as the spherocysts arise around it at the end of twisting hyphae. In *Lactarius* the rose-knots are often simple with one wreath around the central hypha; in *Russula* several simple knots unite to form larger complexes, and the remainders of the collapsing induction-hyphae are observable within these masses.

Corner has also differentiated between those (homoiomeric) tramas where neither skeletal nor binding (ligative) hyphae occur - the monomitic trama structure; the (homoiomeric) trama in which generative and either skeletal or binding (ligative) hyphae occur, the dimitic trama structure, and finally the (homoiomeric) trama in which aside from the generative also skeletal and binding (ligative) hyphae occur. This last type - trimitic - does not occur in Agaricales, and can therefore be disregarded for our present purposes.

Corner (1966) has felt that the term monomitic is a very wide one, and we can only agree with him on this since it includes all those agarics with only one type of hyphae, furthermore all those that have any other structure as long as neither skeletals nor ligative hyphae are present which includes the heteromeric as well as most of the homoiomeric tramas. As a matter of fact, all Agaricales in the classical sense, i.e. all those that do not enter the Polyporaceae sensu stricto (Singer 1962), the Bondarzewiaceae and some species of *Lactarius* are generally monomitic in the sense of Corner's original scheme which has been most widely accepted. However, in 1966 Corner went one step further: He began to distinguish additional types for the "cantharellloid fungi", types he would have formerly called monomitic; thus, by interpreting the fusiform-skeletal hyphae as thin-walled skeletals characteristic for fleshy fungi, he proposed a term "sarcodimitic". It is my opinion that, at least in the present stage of our knowledge, it is useless and even dangerous to press the great variety of trama structures known in the fleshy Basidiomycetes into new rigid terms instead of using the word monomitic (if we have to use a term at all) and merely describe what we see. It appears that Donk (1971, p. 418) agreed with this position. As for further discussion of the matter, the reader is referred to Singer, *Flora Neotropica* 3: 77-78. 1970, 32: 8. 1982; Lentz (1971, p. 111-112); Jahn, *Westfäl. Pilzbr.* 10-11: 231-234.\*

In the Polyporaceae however, the differentiation between mono- and dimitic in Corner's sense becomes interesting and deserves attention. However, I believe with Kreisel that the dimitic trama of Corner's, in order to be meaningful as a character in Basidiomycetes, should be subdivided into: *Dimitic*: Trama composed of

\*The same author, commenting on Aphyllophorales, says "The hyphal structures and the hyphal systems derived from them should not be overestimated as generic characters in taxonomy, in spite of their unchallenged significance; they should not be given priority at any price, a priority they do not always deserve, but should obtain their weight only in connection with other characters" (l.c., p. 234, translated, R.S.). Similar difficulties have been voiced by other mycologists both in Aphyllophorales and Agaricales (Teston, Stankovicova and myself.)

generative and skeletal hyphae in the narrowest sense i.e. "thick-walled, unbranched, aseptate, straight or slightly flexuous, longitudinal ...[hyphae] with the lumen more or less obliterated in mature parts, but the apices thin-walled with dense contents". - *Amphimitic*: Trama composed of generative and ligative (bindung) hyphae i.e. thick-walled, often without lumen, distinctly branched and winding around the other hyphae. We include in this term those tramal structures that contain elements which are ligative only at their distal ends but appearing to be normal skeletals in their lower portion (skeleto-binding hyphae as described by Corner 1981), and also those hyphal systems in which skeletals often but not regularly pass into ligative hyphae. There is in these cases, often observed in *Pleurotus* sect. *Lentodiellum* and *Panus* sect. *Criniti*, a certain fluid transition between dimitic and amphimitic hyphal system. Similar transitions between dimitic and amphimitic hyphal systems have also been observed in Aphylophorales, for example in what Jahn (l.c. p. 224-234) describes as *Trametes cervina* (Schw.) Bres.

In our definition, the family Polyporaceae contains sections and genera with either monomitic (but mostly sclerified) tramal elements, dimitic, and amphimitic trama.

In an extended sense, one might ask whether some strongly elongated, thick-walled, deep-rooting cystidia (or metuloids) do not also qualify as skeletals. If so - and both Lentz and Donk (1971) seem to think that this is theoretically possible - other families but Polyporaceae would also have modified skeletals. Since the latter are defined as hyphae, and the mono-, di-, amphi- and trimitic system refers by definition to the trama only, this aspect is here disregarded. The metuloids of *Geopetalum* (*Faerberia*) are not connected with the skeletal hyphae of the trama (Pouzar, Ceská Myk. 35: 185-188. 1981).

Generally speaking, the tissue of the stipe is usually somewhat denser and more fibrous or cartilaginous, at least in parts, than that of the pileus and the hymenophoral trama, and a sudden transition from the tighter packed hyphae of the stipe to the looser tissue in the pileus may account for what is often described as "pileus and stipe non-continuous", or "distinct", or "separable". There is, however, rarely a sharp line between continuous and discontinuous stipes in the Agaricales, and this character is neither constant nor particularly helpful for determination in most instances. The only case where the separability of the stipe from the pileus is at present applicable with a definite anatomical meaning, is that discovered by Kühner (1926) in *Mycena* where a separation layer consisting of hyphae of a different kind is imbedded between the longitudinally arranged hyphae of the stipe and the larger spreading hyphae of the pileus. The separation layer is probably homologous with the layer separating the stalk and the head of the stilboids in *Mycena citricolor*. It can be used as a specific and sectional character.

In many species we find zones of the context or the entire context gelatinized, i.e. the hyphal walls produce a gelatinous matter into which they are finally imbedded and by which they are separated from each other (Pl. 3; 30). In typically gelatinized tissue, the hyphae of the gelatinous zone are immediately recognizable in 10% KOH mounts by their strikingly loose arrangement, and as a rule, they are thin, and

waving or ascendant\*. There is, however, no sharp delimitation between gelatinized and non-gelatinous tissues, as can be noticed more readily if the gelatinosity of the surface layers of pileus or stipe are studied. We shall see that there is not just a glutinous pileus (with hyphae scattered in the mucus) and a dry pileus, but all kinds of transitional conditions are seen. The same is naturally true about the gelatinosity of the context. Many tissues consisting of thick-walled hyphae produce a slight amount of gelatinous matter and the hyphae are moderately densely arranged. These tissues are interpreted differently by different observers\*\*.

One whole tribe in the Tricholomataceae, viz. the *Resupinateae*, and several genera such as *Campanella* and *Dictyopanus* have partly gelatinous trama. The tissue of most typical Boletaceae is, to a certain degree, gelatinized which accounts for the soft, succulent context characteristic for most representatives of that family as well as related families. A distinct gelatinous layer is also observed in some species of *Crepidotus* (*C. mollis*, *C. uber*, etc.), so conspicuously so that such an astute observer as Patouillard misinterpreted a very old specimen of a tropical *Crepidotus* as a tremellaceous species with holobasidia, and described it as a new genus, *Tremellopsis*, belonging allegedly in the neighborhood of *Sparassis*.

Another interesting structure involving the fundamental and the connective tissue, is that of *Amanita* and related genera of the Amanitaceae. Kühner who justly gives credit to Boudier (1866) for having discovered it, describes it as follows: "In the Amanitas (and in the Limacellas) ... the connective elements are assembled, end by end, into hyphae, as are the majority of the elements, the fundamental ones as well as the connective ones, in the other Agaricales; the fundamental elements of the Amanitas and the Limacellas, however, especially those in the context of the stipe, are isolated and terminal at the tip of the ramifications of the connective hyphae". (Kühner 1945, p. 162.)

In *Mycena* and some related genera, the fundamental tissue consists of hyphae which are unusually broad, relatively short, and constricted at the septae, including the hymenophoral trama and the hypodermium (Pl. 38). This character is of importance in the systematics of *Mycena*-like genera; it was first emphasized by Kühner.

There are also other than fundamental and connective hyphae in the tissues of the Agaricales. They belong to the conducting system and serve for the secretion and excretion of substances, and in a general way, the transport of substances in the carpophore. It is here as elsewhere impossible to always clearly separate these elements from others on a morphological and physiological basis, as it is obvious

\*The mucus forming the gelatinous mass can, in case of doubt, be easily demonstrated by Kühner's method (1933): Dye the sections during several minutes in watery solution of cresyl blue where the walls of the hyphae take a beautiful vinaceous or mauve color but the mucilage remains colorless; one differentiates subsequently in absolute alcohol which dehydrates them at the same time and permits the dye to be fixed on the mucus; to stop the differentiation it is sufficient to pass the sections through xylol; the mucus is then blue.

\*\*Patouillard Lloyd, Dennis, and Singer considered the trama of *Filoboletus gracilis* gelatinized; R. Heim (1946) thinks it is not.

that in many instances the functions are not limited to the specialized organs, or else the specialized organs have often lost their original function.

Heim (1931) has not maintained Fayod's sharp separation between the "laticiferous" and the "oleiferous" type of conducting elements. Yet, Fayod's division is basically correct in spite of the fact that, chemically, they seem to intergrade. It would appear that what "laticiferous hyphae" there are in the Russulas, should, according to the Fayodian terminology, be called "oleiferous hyphae", and they are the ones that according to him originate in the connective tissue, and are continued into the "cystidia" of the *Russulae*. In *Lactarius* and *Mycena* the vessels carrying the latex are called laticifers in a narrow sense, yet the resinous substance responsible for the acrid taste of many Russulaceae is found localized in the "oleiferous hyphae" of *Russula* as well as in the laticifers of *Lactarius*, as can be demonstrated by the acrid taste of the latex in many *Lactarii*. On the other hand, there are *Lactarii* with mild taste and abundant latex. Fayod believed (though he was not certain about it) that the laticiferous vessels actually originate in elements of the fundamental tissue (cf. with this hypothesis Singer, R. *Sydwia* 13: 237. 1959).

Leaving the morphological aspect aside for the present, we are inclined to admit a temporary classification of the types of vascular bodies on the basis of their function and known chemical and physical differences rather than on their supposed origin.

There would then be the following types to be distinguished:

1. *The laticifers in the narrowest sense*. These carry latex, or are homologous to laticifers that do carry latex; they do not necessarily absorb cresyl blue, do not become deep blue throughout the interior, and they do not necessarily become deep blue in sulfovanilline or black in sulfobenzaldehyde. They are not sieve-like on the surface. Example: latex-carrying vessels of *Lactarius volemus*, or *L. nigroviolascens* (Pl. 26; 33).
2. *The oleiferous\* hyphae in the sense of Fayod*. These do not carry latex, but often carry resinous substances associated with an acrid taste of the carpophores, and then they usually turn deep blue in sulfovanilline or brown in sulfoformalin or black in sulfobenzaldehyde. The type of oleiferous hyphae reacting with these aldehydes may turn out to be different from the non-reacting types, yet we take them as being the same, as did Fayod. Examples: (1) of the non-reacting type: *Amanita vaginata* (Pl. 33,1); (2) of the type giving marked color reactions with acid-aldehyde combinations: *Russula emetica*.

3. *The gloeo-vessels, in the sense of Singer (1945)*. These are vessel-like elements attached to gloecystidia projected into the trama and staining deep blue in cresyl blue mounts. Example: *Favolaschia saccharina*. In the Agaricales, they have been

\*The word is somewhat unfortunate since it specifies the contents, yet the contents are complex and variable, and organic "oils" are certainly a minor factor, if at all. However, terms are only words with a definite scientific meaning, and their derivation should not concern us to the degree of proposing changes. This is also the reason why the author is reluctant to give up the term germ-pore as was proposed by Locquin.

observed in *Lactocollybia* (Pl. 33,2). Perhaps, they are also latex-carriers, since in the same genus, a laticiferous species that actually exudes a latex on bruising (*L. lacrimosa*) has been described.

4. *The coscinoids, in the sense of Singer (1947).* These are conducting elements of dark color with a sieve-like surface which is due to winding perforations and holes inside these otherwise solid filaments. The coscinoids (Pl. 31) are found running through all parts and organs of the carpophores of *Linderomyces lateritius* (*Gomphaceae*), proliferating into cystidia-like bodies which are called coscino-cystidia. The latter also exist in at least one species of *Mycena* and in the genus *Boletochaete*.

5. *The chryso-vessels*, hyphae appearing like oleiferous hyphae or gloeo-vessels morphologically but having the same contents as the chrysocystida (golden yellow or lemon yellow, amorphous, rarely guttate or granulose contents when examined in alkali). These are found in some genera of Strophariaceae, especially *Pholiota* and likewise in some species of *Weraroa* (Galeropsidaceae) where they form endocystidia (cystidioid bodies formed in the interior of the trama).

The fruiting bodies of some species are composed almost entirely of conductive elements, i.e. the structural function of the fundamental tissue has been taken over by the elements of the vascular system. Examples of this strange and rare condition are found among the Tricholomataceae (*Lactocollybia*) and also in the ochre-spored group (*Phlebonema*).

The trama, particularly in the close neighborhood of the cortical layers, may also contain endocystidia (as we have already mentioned in the Gastromycetes where this term has been introduced by Singer & Smith 1958). These may belong not only to the chrysocystidium-type, but also to other types like metuloids (Singer 1969, p. 61, *Hohenbuehelia*, and Singer & Clémenton 1972, *Geopetalum*). As for cystidial types see chapter XIV. p. 41-51.

Donk has (1967) renamed my "gloeo-vessels" into gloeoplerous hyphae, but I can see no valid reason why his term would be preferable to an established one (Latin: gloeovasculum), nor can I accept his contention that gloeoplerous hyphae can serve as a substitute for gloeo-vessels and then be subdivided into a series of "subtypes" since such a definition of gloeoplerous hyphae would mean that all elements of the conducting system are gloeoplerous hyphae. Such a word or term is hardly needed, but if it were, its formation would lend itself to ambiguities introducing the same confusion in the trama terminology as has been, unfortunately, introduced into the pseudocystidia vs. gloecystidia complex.

#### XIV. THE HYMENIAL LAYER OF THE CARPOPHORE

##### *The Basidia*

As compared with Aphyllophorales and the heterobasidial orders of the Basidiomycetes, the Agaricales are remarkable for the seemingly uniform shape and development of their basidia. They are all holobasidia, i.e. persistently (but cf. p.

159) unicellular and not divided into what is described as "probasidia" and "epibasidia" (rather inadequate terms). Their position is always\* in a palisade characterized by the approximately even level of the basal septum and the acrogenous sterigmata, the former being the wall between the basidiophorous terminal subhymenial cell and the basidium itself, the latter - the connecting link between the basidium and the spore just before discharge of the latter (usually remaining on the old basidium until its collapse). In all Agaricales, the basidia are standing side by side (or intermixed with pseudoparaphyses), with their longitudinal axis parallel to the longitudinal axis of the neighboring basidia (provided they cover an approximately plane surface such as the side of a lamella). This special type of palisade is called hymenium (Pl. 19; 24; 25; 26; 27; 32; 57h; 63; Fig. 2e). This term is not exclusively used in the Basidiomycetes, nor is it exclusively used for spore bearing surfaces. The apothecia of the Pezizales and related Discomycetes are covered with a similar layer consisting of ascii, and, as will be explained later, the sterile surface of the carpophores of the Agaricales is frequently covered by a hymenium in which the basidia are only a small minority of the elements observed.

Most basidia are clavate or almost so, yet some show a strong ventricosity below the apex which is then broadly capitate and constricted beneath the capitellum, or cylindric to attenuate and broadly rounded at the tip. This latter shape would put them in the category of what is now called the *Urnigera*-type of basidia were it not for the number of sterigmata formed which is always 2 to 4 in these Agaricales whereas it is up to 8 in the Aphyllophorales with typical *Urnigera*-basidia. This false *Urnigera*-type is often found mixed in with normal clavate basidia in the same carpophore, or else some carpophores have the false *Urnigera*-basidia while other individuals have all normal basidia (e.gr. in *Gymnopilus*). According to the author's observations on the nuclear divisions in *Gymnopilus*, this shape is closely connected with the level at which the spindles are formed, and probably a secondary expression of an abnormally low position of the nuclei at the reduction division. A special case of the false *Urnigera*-type is the *Godfrinia*-type, first described by Maire for the two-spored parthenogenetic form of *Hygrocybe conica*.

All Agaricales have chiastobasidia (see p. 111), a term mainly based on the cytology of the basidium, but the chiastobasidium is also characterized by its shape and development. It becomes more broadly clavate when mature, but is fusoid or narrowly clavate when young rather than cylindric-filamentous. Besides, the chiastobasidium is, as a rule, less elongate than the stichobasidium. Within the chiastobasidial group, there is a large degree of variation as to the relative length of the basidia, this absolute length compared with the absolute length of the spores, their absolute breadth in comparison with the length of ellipsoid spores, and the factor ( $F = \text{length} \times \text{width}$ ) of both dimensions of the basidia compared with the corresponding figure of the spores.

\*Kniep (1927) and others indicate mycelial basidia in *Armillariella mellea*; very little is known about their occurrence in other species and genera, and about their cytology as compared with that of the hymenial basidium. The same species and allied forms develop spore-producing endobasidia in the carpophoroids of *Entoloma* (see chapter IV).

Generally speaking, the basidia of the Agaricales with ellipsoid or approximately ellipsoid spores, are about (or often exactly) as broad as the spores are long\*. They are about two to five times as long as the longer axis of the spores, and if longer, they belong to a type that has some taxonomic importance because of its abnormal length. The abnormal length of the *Hygrophorus* basidium, causing the lamellae to be very thick and waxy in consistency, has been used as one of the characters of the family Hygrophoraceae. Some *Tricholomata*, some *Lyophylleae*, the genus *Catathelasma*, some *Mycenae* and *Gerronema ericetorum* along with closely allied species, also many *Amanitae*, are notorious for their longer-than-normal basidia, but they differ from the Hygrophoraceae in other regards. The genus *Laccaria* has thick lamellae but the basidia are not too long as compared with the size of the spores, and it is the thickness of the trama that is responsible for the thickness of the lamellae. The Strobilomycetoideae, among the boletes, are noted for their more voluminous hymenial elements, including the basidia, and *Agaricus*, on the other hand, is characterized by the very small size of the basidia as compared with that of the Strophariaceae and Coprinaceae. Short and thick basidia are characteristic for *Conocybe* (Bolbitiaceae) and *Psathyrella* subgenus *Psathyrella*.

The walls of the basidia are usually thin, and in old specimens and in poorly dried herbarium specimens, the basidia are found collapsed soon after maturity. This is especially true for the Coprinaceae, those with strong autodeliquescent properties, as well as those without them. In the species with tough carpophores, some thick-walled basidia are occasionally found, and even in soft species such as *Armillariella nigropunctata*, occasional basidia with thick walls and a generally sclerotized appearance can be observed. Even if they have distinct sterigmata, they often appear empty, and it may be suspected that a cytological investigation will show them to be pseudoparaphyses. In the *Armillariella*- and *Hygrotrama*-type of sclerified basidia, spore formation can often be observed at the tip of the sterigmata, but, of course, we have not been able to see the spores actually projected. In *Armillariella polymyces*, the "sclerobasidia" were characteristically 7-nucleate (Singer & Cléménçon 1972). Thick-walled basidia of normal function are exceptionally found in some species of the Tricholomataceae (such as *Fayodia*) but in general sclerobasidia are a step towards an abbreviation of the life cycle which will eliminate the spore formation whereby the sclerobasidia become pseudobasidia and function as spores themselves as has been first observed by Heim (1932), and can be seen in most specimens of *Podaxis farlowii*. One step further, elimination of the basidium, leads to bulbilosis.

All basidia in the Agaricales are autobasidia in the sense that heterotropic or orthotropic spores are projected from a half-sickle-shaped sterigma and propelled from the sterigma by an apparatus which is still not fully understood but which, as far as it is understood, has been described by Buller (1909-1937, reprint 1958), Ingold (1953) and McLaughlin in Wells. 1982.

\*In a paper *Studies in the basidium*, E.J.H. Corner points out that, disregarding a few exceptions, the volume of the basidium minus that of the initial vacuole equals the volume of the spore multiplied with the number of the spores per basidium. Further relations see *Gard. Bull.* 26: 193. 1972.

It would be a mistake to think that the apparatus of spore discharge is identical in all Basidiomycetes with autobasidia, and that it requires asymmetric spore attachment and heterotrophic spores. This has been shown by Singer & Grinling in the case of *Hiatulopsis*, an agaricaceous genus from tropical Africa (1967) where the apex (spiculum) of the sterigma eventually becomes sharply recurved outwards and the axially symmetrical orthotropic spore is forcibly discharged by the autobasidium-sterigma apparatus (Pl. 84). This is a type of autobasidium which is not restricted to *Hiatulopsis*, but does not correspond to the type generally described as typical for the "Hymenomycetes". There is no doubt in my mind but that equally detailed observation and experimental data will eventually show that the autobasidium is not a homogeneous and uniform type of basidium.

The order of sequence or maturation of the basidia in the hymenium has been studied by Buller. However, in taxonomy it is not yet accepted usage to rely on more than the two main types of hymenophores named by Buller, viz.

1. *The inaequihymeniiferous type of hymenophore (or carpophore)*. Buller who is not the first to have observed this type is, however, the one who has most thoroughly studied the subject and coined the terms, and therefore his terminology is here accepted (Buller 1922). In the inaequihymeniiferous type, the hymenophore consists of lamellae which are parallel-sided or almost so, rather thin (trama of small diameter), and they are brought into approximately vertical positions through a negatively geotropic stimulus in the growth of the stipe; the lamellae themselves are not always completely vertical, and one side of the lamella may be turned upward while the other side is turned obliquely downward; the hymenium develops unequally on different parts of the lamellae, generally starting to mature at the edge and continuing slowly upwards along the sides of the lamellae; each small area ( $0.1\text{ mm}^2$ ) does not produce a number of successive generations of spores, but all the basidia on the area mature almost simultaneously. The spores are discharged in succession from below upward, and a zone of autodeliquescence follows, destroying completely those parts of the lamellae where the spores have been discharged (Pl. 23; 24, 2).

2. *The aequihymeniiferous type of hymenophore (or carpophore)*. Buller distinguishes this type from the above by the shape of the hymenophore, the development of the hymenium and the manner of discharge of the spores. The hymenophore is lamellate and consists of "gills which are shaped like the blade of a pen-knife". The thickest part of each lamella is attached to the context of the pileus whereas the more or less sharp edge is turned downward; the sides of lamellae are therefore not parallel; a cross-section of the lamellae is wedge-shaped: The lamellae are positively-geotropic during their development, and their median planes are brought into vertical positions, even if the stipe should not be vertical and straight; the younger the lamellae, and the less the angle of tilt, the greater is the success which the lamellae attain in bringing their median planes back into vertical position once this has been altered; consequently, the normal lamella has both sides facing outward and slightly downwards at the same angle. The hymenium, in each small area, develops equally, i.e. the basidia do not mature in zones starting from the edge upwards, and

the production of basidia takes place in succession. During the spore discharge, the hymenophore is not deliquescent.

Buller has not studied the corresponding types in the boletes, but he has subdivided each of his types into a whole series of subtypes which, at present, are not used in taxonomy. This, however, does not mean that a more complete study of the species belonging to each subtype will never furnish any additional taxonomic characters for the distinction of sections, or perhaps even genera. The most important use of this character was made when the generic position of *Pseudocoprinus disseminatus* was investigated (see under *Coprinus*).

The immature basidia, often called basidioles\*, are usually of approximately the same shape as the mature basidia, only often slightly to considerably smaller, or narrower (Pl. 79hy) or rather more fusiform than clavate. Fusiform basidioles, are rather characteristic for certain genera, such as *Marasmius*, *Marasmiellus*, *Crinipellis* and *Collybia*, also certain smaller tricholomataceous genera, related to these four (Pl. 63, 2b, d, e; 64, 2bl).

In most species of the inaequihymeniiferous type and in but a very few of the aequihymeniiferous type of agarics, the basidia are separated by and dispersed in a more or less regular manner, among pseudoparaphyses (Pl. 23, 24, 2). Or, as Buller describes this situation for the inaequihymeniiferous type and the *Psathyrella*-

\*Boudier and Romagnesi use this term for what we call pseudoparaphyses, or aborted basidia; and Petrak uses the word pseudoparaphyses for a certain type of paraphysoids in the Ascomycetes. We use the word basidioles in the sense in which it is used by most cytologists and taxonomists in the Agaricales, i.e. as term for the young binucleate basidium with meiosis; the following stage, during the nuclear divisions has been called metabasidium by Donk but this term is also used in a somewhat different sense in other groups of fungi. The word pseudoparaphyses is here used exclusively for the consistently sterile, often slightly modified (subvesiculose, broadly clavate), non-protoplasmatic basidia, since in the Myrangiiales the term paraphysoids (remainders of the interthelial stroma) is perhaps sufficient and satisfactory. - Heim attempts to apply the term basidioles to both young basidia and pseudoparaphyses ("they constitute basidia which are young or arrested in their development"). Lentz (1955) follows his example. The lumping together of two different things under a single term leads, in my opinion, to confusion and should be avoided.

The word pseudoparaphyses as used in Basidiomycetes is limited to basidiomorphous broad, "empty" bodies which are very well developed in some Coprinaceae and near the edges of the lamellae in some Bolbitiaceae, particularly in *Bolbitius* and *Conocybe*. It can therefore not be used for the truly paraphysis-like sterile bodies found in the hymenium of some Corticiaceae, Favolaschiaceae, as well as in many genera of Heterobasidiomycetes. These organs are filiform and sometimes monilioid; they are known under the special terms pseudophysyses (Litschauer 1907), dicaryoparaphyses (Lowy 1954), hyphidia (Donk 1956), and are related to the (more branched) dendrophyses in the narrower sense, i.e. excluding the acanthophysyses. While dendrophysoid bodies occur in the agarics (e.gr. *Crinipellis*, *Mycena*) as cheilosystidia (and this term is here sufficient) we have not observed hyphidia in Agaricales except for extreme cases of narrow cystidia (see there, below) which are never exclusively and persistently pseudophysoid but may in certain cases vary to include some individual cells that might be characterized as pseudophysyses-like. True pseudophysyses have not been described in Agaricales. But massed together in bundles, they do occur as "pegs", see p. 49-50. For a more detailed discussion of the terms paraphysis, pseudoparaphysis, paraphysoids see Singer & Gamundi (*Taxcon* 12: 147-150. 1963). Donk (1964) believes that pseudophysyses should apply only to the "pseudocystidioid" or "gloeocystidioid" bodies for which they were first proposed. This would make hyphidia an acceptable term (erroneously changed into "hyphoids" by A.H. Smith in Ainsworth & Sussman 2: 176, 1966 and inadequately defined).

subtype of the aequihymeniferous type, pseudoparaphyses "are normal constituents of the hymenium. They are very large and are united so as to form a pavement through which the basidia protrude. They not only support the basidia mechanically but act as space-makers so that adjacent basidia are separated from one another by a distance just sufficient to prevent any jostling during spore development and spore discharge" (3: 122. 1924). This arrangement of the basidia is paralleled by a definite dimorphism, more rarely a trimorphism, or tetramorphism of the basidia, expressed in the distance by which they project above the pseudoparaphyses, their shape and the time at which they develop - the least projecting basidia being the ones that belong to the latest generation. All these characters are included when a hymenial structure is called coprinoid. The coprinoid hymenial structure (Pl. 24, 2) is among the characters that distinguish *Coprinus* from *Psathyrella*.

Of all these characters, Fries concentrated his attention on the only one that is macroscopically visible, viz. the autodeliquescence. However, the autodeliquescence is not understandable unless the shape of the lamellae in *Coprinus* is taken into consideration. The equal diameter of the hymenophoral trama makes spore dissemination difficult. In those species that have endocarpous development and toughish consistence, the problem is solved by postponement. In the ephemeral species with agaricoid, i.e. non-endocarpous development, and fragile consistency, the problem can be solved in two ways, either by transformation of the lamellae into wedge shaped formations - or by autodeliquescence, i.e. by removing the lower part of the lamella that would hinder the free fall of the discharged spores, from the zone immediately above. At the same time, the spores that have accidentally stuck to the hymenium or have not come clear from it, are suspended in a fluid that drops onto the grass, or is taken off by passing animals, hereby receiving a second chance of dissemination. Both the wedge-shaped lamella and the autodeliquescent lamella are realized in the family Coprinaceae. Since animals play a certain rôle in the latter type of spore dissemination, it is not surprising that the truly inaequihymeniferous *Coprini* are often found on animal excrements, such as horse manure, rabbit-, deer-, and cow dung, etc., and also on manured fields, white-mushroom beds, and manure heaps.

### *Cystidia*

The word cystidia (cystides, Léveillé 1837) in its broadest sense - replacing the earlier term "Michelian bodies" (so called for their discoverer, the early Italian mycologist Micheli) - designates any sterile bodies that are interspersed in the hymenium or replace the basidia in any part of the hymenophore, or - according to later emendations of the term - occur on one of the usually sterile surfaces of the carpophore but resemble the hymenophoral cystidia which are apparently homologous with them. However, this traditional definition of the cystidia, has recently been - step by step - abandoned in favor of narrower terms. Since the presence or absence of cystidia in the broader sense is not always a constant character, a dif-

ferentiation between the various types of cystidia is desirable from a taxonomic point of view as well as from a purely morphological, anatomical, and physiological viewpoint.

The main classification of these sterile bodies in the concepts of some authors derives from the distribution of the cystidia on the carpophore. Some authors use the terminology of Buller which we think is rather superficial and not truly morphological though its simplicity has much to recommend it. For this reason we mention it here. It divides the cystidia into the following categories: Cystidia A. on the hymenophore (a) on the sides of the lamellae or the interior of the tubes: *Pleurocystidia*. - (b) on the edge of the lamellae or pores: *Cheilocystidia*. - B. on the sterile surfaces of pileus or stipe (a) on the pileus: *Pilocystidia*. - (b) on the stipe *Caulocystidia*.

This scheme calls pilocystidia the cystidia-like bodies on the epicutis of the pileus in *Russula emetica*. If exactly the same type and subtype of bodies occurs on the stipe of *Russula emetica*, it is called caulocystidia. However, entirely different cystidia-like bodies occurring on the pileus of *Flammulina velutipes* are given the same name as those occurring on the pileus of the *Russula*; and the elements of cystidia-like appearance found on the stipe of *Leccinum scabrum*, though quite different in shape, chemical characters, and origin from those of the *Russula*, are called caulocystidia in the *Leccinum* as well as in the *Russula*. Actually, the pilo- and caulocystidia of the *Russulae* are homologous and practically identical whereas the pilocystidia of *Flammulina* and the caulocystidia of *Leccinum* belong to very different types. Furthermore, cystidia occurring on the surface of the peridium of the Secotiaceae are often homologous with pilo- and caulocystidia of related genera of Agaricales. They can not logically be called either pilo- or caulocystidia.

Caution with regard to Buller's terminology is also necessary when the cheilocystidia are considered. If a cystidium of the same type as those of the sides of the lamellae and interior of the tubes also occurs, unmodified, on the edges or pore orifices, even if this should be the case in different density, it is, morphologically speaking, not a different type of cystidium, but a fully homologous cell which should not be called cheilocystidium even if the topographical aspect is emphasized. A cheilocystidium is a sterile cell or morphologically differentiated type which is not homologous with the pleurocystidia or else occurs on the edge (and sometimes its immediate neighborhood) exclusively while the sides of the lamellae (or the tube interior) are devoid of cystidia. Examples apt to illustrate this point are the excellent *Inocybe*-descriptions given by J. Favre (1955, 1960) since they show that confusion is likely to result where the "topographical" aspect is overemphasized whereby the metuloids occurring at the edge of the lamella are confused with the differentiated (thinner-walled, shorter, broader) cheilocystidia characteristic for most species of *Inocybe*. This becomes particularly confusing in such groups as *Pluteus* section *Pluteus* where the cheilocystidia are always thin-walled and the metuloids near the edge may be somewhat differentiated with regard to those growing near the inter-lamellar spaces, but are still not cheilocystidia. Even if occasional transitional bodies can be found aside from the cheilocystidia and the two types of metuloids, the edge-near metuloids should never be described as cheilocystidia.

The origin of the cheilocystidia is not always and not even predominantly - as sometimes claimed - due to an extension of the terminal cells of the cuticular elements passing over the margin onto the edges of the lamellae. *Inocybe tricolor* provides an excellent example where the presence of two to four sterigmata on occasional cheilocystidia shows convincingly that these are actually of basidial origin, being basidioles which have lost their function and have, at the same time, become morphologically slightly differentiated and localized. By the same token, the "monosporous" or "bisporous" capitate cheilocystidia of *Conocybe* or, for that matter, of *Hohenbuehelia*, are of basidiole origin, inasmuch as they appear only exceptionally on the hymeniform layer of the pileus but frequently on the surface of the stipe, and always only when there are extrahymenial basidia present.

Those cystidia-like bodies that are found in the hymenophore, on the edge as well as the sides of the lamellae of many *Russulae* and *Lactarii* should be put in a category by themselves because of their origin in (or homology with) the conducting system of these genera. By their very nature, they are merely prolongations of the conducting system into the hymenium, or into the epicutis of the pileus or the covering layer of the stipe. This kind of cystidia has been called pseudocystidia by Kühner and by Romagnesi. They were first recognized as "false cystidia" ("simulant des cystides") by Boudier (1866). We apply the term pseudocystidia as a general name for all cystidia derived from conducting elements, whether they otherwise belong to the laticiferous system, or oleiferous hyphae, or the gloeo-system, or the coscinoids.

Pseudocystidia are common in the Russulaceae, in *Lactocollybia*, in *Macrocytidia* and the Bondarzewiaceae, as well as in some species of other genera such as *Rhodocybe*, *Fayodia*, *Hydropus*, *Phyllobolites*, *Boletochaete*, etc. In each of these cases, however, the type of pseudocystidia occurring is different, and has received different names. The subtype found in the Russulaceae and *Lentinellus* is known as macrocystidia (Romagnesi 1944; Plate 21, 4). It is characterized by a chemical feature, viz. the discoloration with acid-aldehyde solutions, and the weak absorption of cresyl blue by its contents. Another subtype has for a long time been known as gloeocystidia; however, the existence of gloeocystidia in Agaricales was not known until recently. It is found in *Russula polyphylla* and probably also in some other species of the Russulaceae, in *Lactocollybia* (Pl. 20, 3), etc. The gloeocystidia can be recognized by the oily contents that are often very distinct but sometimes absent, and, more clearly, by the deep blue color they assume when stained with cresyl blue (excepting the walls which remain a pale violet color). This metachromasy is, on the basis of what is known at present, an infallible sign that the bodies showing it are part of the gloeo-system or, more precisely, gloeocystidia\* (Pl.

\*The term gloeocystidium has been subject to much diversity in definition. The first to specify and restrict the term was Heim (1946) who was followed first by the present author, and later on by the majority of agaricologists. However, some authors wish to use the term in a wider sense, some in so wide majority of agaricologists. However, some authors wish to use the term in a wider sense, some in so wide subordinating the pseudocystidia under the gloeocystidia. Romagnesi wonders whether macro- and gloeocystidia are not the same. They may be (in certain Russulae of the Foetentinae group) in the sense that a pseudocystidium in a specific case may be a macrocystidium and a gloeocystidium at the same time. One should not be confused by the fact that the genus *Macrocytidia* has no macrocystidia but gloeocystidia.

21, 3). The third subtype is rare, and it is called coscinocystidia because of the sieve-like character of their surface. They are protruding cystidial-like ends of the coscinoids and have first been observed in *Linderomyces* (Gomphaceae, Aphyllophorales Pl. 31) but have also been observed in several species of true Agaricales, especially *Boletochaete* (Boletaceae). Petersen (1971) thinks that they are in cases observed by him nothing but final stages of gloeocystidia. But even so, a special term for this condition - whether it is a stage of some other type of pseudocystidium or not - is appropriate.

A further distinct type of pseudocystidium has been discovered by Cléménçon (Singer & Cléménçon 1972, Cléménçon 1972) and has been called phaeocystidium (Pl. 56). Phaeocystidia characterized by granular internal bodies, coelosphaerites, which in the light microscope merely show as a homogenous to finely granular light-brown content which in Melzer's reagent becomes darker golden brown, but in EM sections they are electron dense, round, with a central hollow space (Pl. 56). They occur only in one monomorphic subgenus of *Fayodia* (*F. deusta*), as far as we know now.

Another type of pseudocystidia may be seen in the cystidia of *Resinomycesena*, *Baeospora myosura*, *Physalacria andina* and other species, *Gliocephala allomorpha* and other species, *Suillus amabilis* and other species which are evidently excretory and incrusted by a resinaceous more or less colored crust. In *Baeospora* has this type of cystidia been studied carefully (Cléménçon 1972) and it appears that the resinaceous excretion is formed in the endoplasmatic reticulum (ER) of the cystidium and finds its way through the cystidial wall to form an incrustation, together with the mucus of the cell wall which is not solid but flows downwards below the excretion zone proper. The cystidia of *Physalacria* which are here classified tentatively in the same group of cystidial types because of the similarity of the cystidia and their excretion, have been called oleocystidia by Corner (1950) - a term I accept with a certain reluctance because our knowledge of the chemical nature of the excretion does not warrant the implication suggested by this term. The origin of these cystidia is not the conducting system but it appears that they originate from subhymenial and trama hyphae which are morphologically not differentiated.

Those pseudocystidia that are obviously terminal bodies of the laticiferous system of the trama and enter the hymenium in a more or less (morphologically) differentiated form, do not always have the chemical characteristics of the macro- or gloeocystidium, and may then be referred to as lacteocystidia (Locquin 1953), often a temporary term since frequently these pseudocystidia have the characteristics of macro- or gloeocystidia, and will eventually be called by a name given to other subtypes of the pseudocystidia.

In certain cases we find that typical macrocystidia or gloeocystidia originate not from portions of the conducting system but become excretive (and thus, in a manner of speaking - part of it) at the very septum that separates them from the next-lower hyphal cell, or in certain cases, they become, theoretically, part of the conducting system from a certain level of the cystidium itself as in *Russula nauseosa* where only

the apex of the macrocystidium turns blue in sulfovanillin and black in sulfobenz-aldehyde. Typical for this kind of unorthodox pseudocystidium is also often the chrysocystidium, characteristic for *Naematoloma fasciculare*, *Pholiota astragalina*, and many other species of the Strophariaceae which are often continued into hyphae with similar contents (amorphous bodies, more or less yellowing in NH<sub>4</sub>OH and KOH\* but just as often, or oftener pass directly into ordinary hyphae (Pl. 22, see also p. 38).

These cystidia, with an excretive function or otherwise analogous to typical pseudocystidia, are here treated together with the typical pseudocystidia. Another example is that of the deep-rooting cystidia of the type found in *Geopetalum*, *Panus* section *Panus*, *Pleurotus floridanus* and in *Hohenbuehelia*, in *Inocybe*, *Galerina* section *Inocyboides* and many other groups of Agaricales. The same type of cystidia is also found in *Peniophora* (Aphyllophorales) and is called metuloids by Cooke (1879). These bodies start out by being pseudocystidia in the sense that they appear to be proliferations of the conducting system into the hymenium (yet, neither belonging to the subtype of the macrocystidia, nor the gloeocystidia, nor the coscinocystidia) and serving as excretive organs. This stage is easy to observe and long preserved in *Geopetalum*. Later on the metuloids become thick-walled, lose their excretive function and strongly resemble the leptocystidia - were it not for the fact that they are uniformly deep-rooted, uniformly thick-walled and mostly hyaline to grayish straw-colored. Deposits of coarse crystals are often found even on the old metuloids, especially at the apex but sometimes all over. This kind of cystidium has often been called "Peniophora-cystidium" by mycologists (including this author) but the term metuloids appears to have priority, brevity, precision and descriptiveness in its favor. Romagnesi (1944) calls it "lamprocystide"\*\*\*.

The metuloids or metuloid cystidia in this definition can be subdivided into five subtypes:

- (1) Inamyloid metuloids, strongly metachromatic in cresyl blue mounts (e.gr. in *Campanella*) - the most common subtype (Plate 57 Met.).
- (2) Inamyloid metuloids, not metachromatic in cresyl blue mounts, the *Inocybe*-subtype (e.gr. in the cystidiate *Inocybes*, Pl. 18).

\*This internal body can also be stained with ferric acetocarmine as used for the *Lyophyllum*-basidia (see below, p. 111). Romagnesi stains it with a colorant known in France as bleu C 4 Poirrier (cotton blue). This can be replaced by water blue Geigy according to Jossérand. These blues are mixed on the slides with a few drops of lactophenol (Amann). A very useful dye for the chrysocystidia is also patent blue V 0.1% watery solution, see Hostettler (*Schw. Zeitschr. Pilzk.* 57: 92-93. 1979) and Jahnke (Mycologia 76: 940-943. 1984). In some chrysocystidia the internal body is hyaline or pale citrine (f. ex. in a few species of *Psilocybe*, in *Anellaria*). The typical yellow chrysocystidia were once termed "Naematolomoid type of cystidia" by A.H. Smith (1951) and this term has perhaps still some meaning if it is used to distinguish the "true" (yellowing in alkalis) chrysocystidia from the non-yellowing type.

\*\*Donk was the first to follow Cooke and suggested a revival of the term metuloid, but when he finally published his observations on the terms metuloids and lamprocystidia, he preferred lamprocystidia. In view of the wide acceptance of the term metuloids in the current literature, and the early history of this term, it is suggested here that those who would like to continue using the term lamprocystidia, might use it for the type of cystidia Romagnesi (1944) had foremost in his mind, the *Inocybe*-subtype, in distinction from other subtypes.

(3) Pseudoamyloid metuloids, metachromatic in cresyl blue or toluidin blue mounts, the *Geopetalum*-subtype (e.gr. in *Geopetalum carbonarium* (Pl. 2) and some *Crinipelleae*, less pseudoamyloid in *Gliocephala inobasis*, *Marasmius pseudoniveus* var. *amylocystis*).

(4) Amyloid (dermato-)metuloids occur in *Deigloria anastomosans*.

(5) Colored metuloids (almost setoid), the *Copelandia*-subtype (e.gr. *Copelandia cyanescens*), Pl. 77, 2, also occurring in *Agaricochaete*.

The metuloids of *Copelandia cyanescens* bring up the question whether there is a clear limit between the metuloids and the setoid cystidia. Setoid cystidia are thick-walled cystidia which have distinctly acute tips and colored wall. Such cystidia have been found in certain boletes (*Tubosaeta*, Pl. 20) and *Marasmius* (*M. cohaerens* and related species). They have been called setoid cystidia because of their similarity to setae (hymenial setae) from which, in the sense of those working in Aphyllophorales, however, they are basically different. They are much rather comparable to pigmented hymenial skeletal hyphae. Whatever they are, they differ from metuloids mainly by the absence of an excretive function (or the absence of data to demonstrate such a function). Mycologists are free to use the term setoid cystidia whenever they feel they have no evidence for or likelihood of excretory function, as long as the walls are pigmented by an intraparietal pigment.

The remaining subtypes of pseudocystidia have not been named separately, and are characterized by three negative characters (1) by not darkening with acid aldehydes (2) by not having completely deep blue contents when dyed with brilliant cresyl blue (3) by having an entire rather than a sponge-like interior. These subtypes of pseudocystidia should at present be referred to in a general way, as pseudocystidia or pseudocystidial stages of certain other types of cystidia (*Rhodocybe*, *Asproinocybe*, *Porphyrellus*, *Psathyrella* section *Heterocystis*, etc.).

All organs in the Agaricales that answer the general description of cystidia but do not fall into the category of pseudocystidia, are true cystidia.

Not all true cystidia have their origin in the deeper layers of the subhymenium, or in the trama. Some originate at exactly the same level as the basidia, and differ from the basidia and pseudoparaphyses merely in size and/or shape. These are called cystidiolae (Boudier, = "Hymenialcystiden" of Van Overeem). True cystidiolae are frequently found on the sides of the lamellae or in the interior of the tubes of certain Agaricales - all taxa - and in certain groups they are rather characteristic. If they occur on the edge of the lamellae and lamellulae, excepting the attenuate portion of the latter, or the pores exclusively, they should be referred to as cheilocystidia (Buller 1924). We cannot believe it necessary or advantageous to differentiate between the cheilocystidia that are, according to the position of their mother cell, localized cystidiolae, and those that derive directly from the trama because of the lack of a subhymenial layer at the very edge of the lamellae as is often observed in *Collybia*\*. The "pleurocystidia" of many species or varieties of *Crepidotus* appear

\* The cheilocystidia of *Collybia peronata* and related species are also remarkable for their development which seems to be retarded; they are much more inconspicuous and scattered in young specimens than in mature carpophores.

to be misformed or aborted (cytologically malfunctioning) basidia or basidioles, and occasionally have been observed (Singer 1971) to "germinate" by apical outgrowths which continue into clamped hyphae, e.gr. in old specimens of *C. caspary* where few fertile basidia are found among the cystidioles. In *Marasmiellus* cystidioles are much more frequent in specimens with many bisporous basidia or in clamp-less species. If cystidioles are misformed or aborted basidioles - and if, as seems quite probable - this assumption can be generalized, there is good reason to distinguish between basidioles and cystidioles, and between cystidioles and other types of cystidia. The only morphological difference between cystidioles and leptocystidia - the basidia-like aspect and the origin on the same branching subhymenial hypha as the basidium - must be interpreted as meaning the basidium and the cystidiole are formed later than the leptocystidia (true cystidia).

Another category of true cystidia (Pl. 27, 1; 57, cy; 66, hc; 70, c; 71, cy, pl) has its origin in the tramal hyphae, or, in some cases in the lower part of the subhymenium, at a deeper level than the basidia. Except for their deeper origin they do not essentially differ from the cystidioles in their development but in their non-resemblance to the basidia. The cystidia of many boletes come into this category (Pl. 25; 76, 12) and since it appears that Romagnesi (1944, p. 15) calls these *cystides vraies* "leptocystidia" I have accepted this term since it is more precise than "true cystidia".

The very voluminous cystidia of some Coprini, with thin wall and easily collapsing also belong in this category, and perhaps likewise those of *Volvariella*. They often originate in the lower part of the subhymenium or the outer part of the hymenophoral trama but seem to have a mechanical function: they touch the hymenium or cystidia of the opposite lamellar surface acting as some sort of pillar or cushion keeping the young hymenia of neighboring lamellae apart. It goes without saying that leptocystidia of this kind can occur only where the lamellae in the young carpophore are crowded. In *Volvariella* the cystidia have also the function of hydathodes (Thielke, *Zeitschr. f. Myk.* 49: 257-260. 1983).

Obviously, there are cases where a partial thickening of the wall in mature cystidial cells produces cases intermediate between leptocystidia and metuloids. *Chroogomphus jamaicensis* with locally but constantly thickened wall has resinous incrustations both on the inside and outside of the wall, and should be treated as of the same category as the cystidia of *Baeospora*, viz. "oleocystidia" in the sense of Corner (Pl. 75, 7).

The leptocystidia constitute one of the most frequently encountered and diversified types of sterile bodies in the hymenium, and it may be expected that certain characteristic subtypes will be distinguished in the future. Nevertheless, this should not be attempted before more detailed data are available about the function, chemistry, and fine structure of these cells.

Sometimes undifferentiated and unmodified hyphae break through the hymenial surface and form dense pyramidal or otherwise fasciculate bunches of hyphae differing from both cystidia and pseudocystidia in the fact that they arise from several hyphae and are septate. Their function, if any, is unknown. They are

hyaline, or pigmented (as in *Mycobonia*). They may be compared with hyphids or pseudophyses, but they do not function as forerunners of the basidial layer (as in a catahymenium), nor do they form a continuous trichodermium or palisade. They are found most frequently, and in some species constantly, in the family Polyporaceae. Polypore specialists have called them "pegs", a term accepted by Bondarzew & Singer and Singer (1951) for both Aphyllophorales and Agaricales. Imai calls them *spinae* (which should not be confused with the hymenophore of the hydnaceous type).

Certainly, there are, often in a single section of a specimen, certain cystidioid cells in the hymenium which, constituting a minority, are apparently transitional between two types of cystidia occurring in that particular species. Such transitions have been found by me for example in *Pluteus*, between the metuloids of the edge-near zone and the cheilocystidia; between the cystidioles and pseudocystidia in *Melanoleuca* (Pl. 21, 5), between macro- and gloeocystidia in *Russula polyphylla*, between basidia and cystidioles in *Omphalotus olearius* and *Gerronema venustissimum*; between setoid cystidia and leptocystidia and between lepto- and gloeocystidia in tropical species of *Marasmius*, etc. If such cases were taken as weakening the terminology and in an effort to suppress certain terms in favor of others and for this very reason (transitions) alone, we would have to return to the old term "Michelian bodies".

It is furthermore impossible to accept rash and personal redefinitions of defined terms or vaguely defined new terms or simply new words meant to substitute for older ones. It is much better to refrain from being too precise in cases where the true nature of a cystidial cell or body is not sufficiently known in order to give it any of the more modern terms. The best way to deal with these cases is to simply refer to them as "cystidia" and give all the descriptive data actually at hand.

This cannot be done in the case of the pseudoparaphyses since it would indeed be confusing to call them "cystidia" (see p. 42, 118). Singer & Gamundi (1963) have given a full account of the history of the term pseudoparaphysis as well as the term paraphysis, paraphysoid, etc. The echo in various articles published subsequently in *Taxon* showed a wish that "paraphysis" be used in two different non-homologous meanings. I cannot understand why this should not also be feasible for the term pseudoparaphysis, if indeed - which is still doubtful - the term is needed in Ascomycetes. In Basidiomycetes the term is used since 1926 (not since Romagnesi 1944 as Donk implies) and those who wish to replace it by another (brachycystidium, brachybasidiole) cannot make up their minds, rightly so because both substitute terms are badly constructed, the pseudoparaphysis not being a cystidium nor a basidiole.

Summing up the foregoing discussion, we have the following survey of sterile bodies in the hymenium:

1. Hyphal cells: *Pegs*.
2. "Pavement" elements, basidiomorphous, separating the basidia in inequimy meniferous carpophores: *Pseudoparaphyses*.

3. Young, immature basidia: *Basidioles*.
4. Differentiated (from basidioles and pleurocystidia) cystidiform cells making up (interspersed with basidia and basidioles, or not) the terminal cells of the edge of the lamellae or pore orifices: *Cheilocystidia*.
5. Hymenial extensions of the conducting system and other excretive cells in the hymenium, as well as homologous cystidia with chemically heterogeneous contents: *Pseudocystidia*:
  - A) Pseudocystidia carrying latex: *Lactecystidia*.
  - B) Pseudocystidia with metachromatic oily contents in cresyl blue: *gloeocystidia*.
  - C) Pseudocystidia with an amorphous body or bodies in the contents, generally yellowish in KOH or NH<sub>4</sub>OH mounts: *Chrysocystidia*.
  - D) Pseudocystidia with brownish contents, weakly pseudoamyloid, containing coelosphaerites: *Phaeocystidia*.
  - E) Pseudocystidia turning blue in sulfovanillin, black in sulfobenzaldehyde, with granular to banded contents: *Macrocytidia*.
  - F) Pseudocystidia with a sponge-like body and/or sieve-like surface: *Coscinocystidia*.
  - G) Thick-walled (when mature) pseudocystidia with presumably excretory function in all or part of their development, often rising from oleiferous hyphae and sometimes accompanied by endocystidia (metuloid): *Metuloids*.
  - H) Pseudocystidia producing corpuscles in the interior which after passage through the thin or partially thickened wall form a resinaceous incrustation (often pigmented and semi-solid, eventually often fragmented and shed from the main body): *Oleocystidia* (a temporary term, in the sense of Corner).
  - I) Other types of pseudocystidia rising from oleiferous hyphae and characterised by optically or chemically differentiated content or incrustation.
6. Morphologically differentiated but basidiomorphous sterile cells rising from the same terminal subhymenial cell as the basidia, and occurring on the sides of the lamellae as pleurocystidia (exclusively or accompanied by identical cells at the edges or pores of the hymenophore): *Cystidioles*.
7. Cystidia not falling into one of the categories indicated under 1-6, usually more strongly differentiated than the cystidioles, usually rising from a level lower than that of the basidia, generally thin-walled, and not restricted to the edges of the lamellae or the pore orifices: *Leptocystidia*.
8. Cystidia without known excretory function and with thick, strongly pigmented wall, with seta-like appearance: *Setoid cystidia*.

Since the distribution of the cystidia is often different on the edge of the lamellae and pores or contrasted to the sides of the lamellae and interior of the tubes, Maire has proposed to call the edges:

1. *Heteromorphous*, if they are sterile (or predominantly so) because of the presence there of a type of cystidium (cystidiole) that does not occur on the sides of the lamellae (or in the interior of the tubes). We may logically designate as inversely heteromorphous the opposite case where the edge alone is completely free of cystidia.

2. *Subheteromorphous*, if the edges are sterile (or predominantly so) because of the density of the same type of cystidia that is scattered among the basidia on the sides of the lamellae (or the interior of the tubes).

3. *Homomorphous*, the hymenium on the edges is not in any way different from that on the sides.

This terminology is also applicable to the pore orifices.

Romagnesi (1944) has suggested the term "pseudoheteromorphous" for those cases of heteromorphism where the cystidia occur only on the edge without being homologous with any dermatocystidia ("hairs"), as is the case in *Psathyrella candoliana*. The term "pseudo-heteromorphous" is based on the somewhat precarious differentiation of two types of what is here called cheilocystidia, viz. those cheilocystidia that are comparable with the "hairs" of the cortical layers (of pileus and stipe) rather than with hymenial cystidia, and those that are not. The fact that the hymenium is, in many primordial and young stages of agarics and boletes extended beyond the hymenophore proper, makes it very difficult to justify this differentiation on a morphological basis\*.

Some terms frequently used in descriptive agaricology still need a word of explanation. The sterigma-like prongs or knob-like excrescencies at the very apex of the cystidium are called mucro if only one central one occurs. If several occur, they are usually referred to as appendages or setulae (the latter term preferred in the marasmoid fungi where they are often pigmented by an intraparietal pigment, and the whole cystidial cell is called broom cell, celle en brosse). If all setulae are more or less erect and apical, we refer to a broom cell of the Siccus-type (because *Marasmius siccus* has them, Pl. 59, 6, 8), but if they are divergent, usually short, and descending from the apex down towards the middle of the cell, they are of the Rotalis-type (*Marasmius rotalis* being characteristic for this, Pl. 59, 2, 5). The broom cell without the setulae is called the main body of the cystidium. Knob-like to long-effilcate appendages can be found in any number on the apex and/or the sides of the main body.

Some similar type of cystidia and cheilocystidia is also diverticulate like the Rotalis-type of cystidia but differs in not being "broom-cell"-like because it is not necessarily subisodiametric but sometimes smooth over the apex, or separating from their mother-cell. These cystidia or cheilocystidia (Pl. 71, 1, ch) are called acanthophysoid, or simply diverticulate. In the genus *Mycena*, in particular we find all transitions between acanthophysoid-diverticulate and Rotula-type cystidia, cheilo-

\*Josserand (1952) comes to a likewise negative result regarding Romagnesi's terminology, following an independent and different line of thought; he uses the term "cheilocystides" for both "cystides marginales" and "poils marginaux".

cystidia, or broom cells. Similar cells, usually as cheilocystidia, are also found in the Favolaschiaceae (Aphyllophorales). Other non-entire cystidia and cheilocystidia show a certain tendency to ramify apically, laterally, or basally, and are then described as "dendrophysoid", "antler-like", or having a "Rameales-structure" (e.gr. Pl. 58, 2ch; 80, 2).

The undivided cystidium of all types and the main body of appendiculate cystidia occurs in the Agaricales in a very wide range of shapes and the shape may be variable or very constant and characteristic. The most common shapes are filamentous, ventricose to fusoid, ampullaceous (bottle-shaped), subulate, clavate, with or without a slight to strong constriction in the upper or mediane zone, more rarely in the lower portion of the cystidium. Frequently the cystidium is pedicellate, i.e. a hyphoid continuation of the widened portion of the cystidium to the last septum is strongly developed or conspicuous.

Some cystidia are almost imbedded in the hymenium or barely reach the level of the sterigmata. Such cystidia, if thin-walled, are often difficult to discover. Others project, sometimes considerably beyond the level of the basidia. Their size may be so noticeable that the lamellae under a good hand lens appear as distinctly spinulose-pilose as the hymenial surface of a *Hymenochaete*. Their length may reach 300 µm.

The presence or absence, type, distribution, color, shape and size of the cystidia are important diagnostic characters in all taxa. Cystidia (in the widest sense) are absent in none of the families of the Agaricales; but they are present in all species and genera of the Gomphidiaceae and Russulaceae and in all Boletaceae. Metuloids are characteristic as a generic character in *Hohenbuehelia*, *Geopetalum*, as a sectional one in many genera. Macrocytidia are found in the Russulineae only. On the other hand, nearly all cystidia (in the widest sense) enumerated and defined in this chapter seem to occur, without much modification, also in either the Gasteromycetes or the Aphyllophorales, or both. Thus, we find macrocystidia in *Lentinellus* (Aphyllophorales), and other genera of Aphyllophorales as well as in some Hydnangiaceae (Gasteromycetes), to give only two examples. Only the phaeocystidia have not (yet?) been discovered in any genus other than *Fayodia* (Agaricales).

## XV. THE STERILE TISSUE OF THE HYMENOPHORE

The hymenium is only a thin outer layer of an organ usually referred to as hymenophore, i.e. a part of the carpophore which is modified and especially adapted to provide a maximum of surface space for the hymenium and thus for the formation of a maximum number of spores. Hymenophore is the general expression for all kinds of hymenium-bearing organs whether they appear as lamellae (gills) or tubes with pores, veins, or tramal plates enclosing chambers or loculi, or (but not in the Agaricales) spines or teeth-like formations, splitting or concentrical lamellae etc.

Some Agaricales are devoid of a hymenophore either only in youth (hymenophore formed late when the hymenium has already begun to sporulate) or through all

stages of development. The hymenium covers then what is called a smooth hymenial surface as in clavarioid fungi and what classically was termed Thelephoraceae in the Aphyllophorales and the so-called reduced or (in the widest sense) cyphelloid forms and genera of the Agaricales. The classical family Agaricaceae (now reduced to the genus *Agaricus* sensu stricto and allied genera) was characterized exclusively by normal, waxy, radiating lamellae. In the present view, the Agaricales are not the only order which contains a lamellate hymenophore, but lamellae do occur also in the Aphyllophorales and Gasteromycetes. Lamellate forms which have been excluded from the Agaricales for many years are *Lenzites*, *Gloeophyllum*, *Xerotinus* (Pl. 42), *Montagnea*, *Galeropsis*, *Panaeolopsis* (the first three belonging to the Aphyllophorales, the last three to the Gasteromycetes). In the present edition we have excluded also *Schizophyllum*, *Lentinellus* (to Aphyllophorales), and *Gastrocybe* (to Gasteromycetes).

The sterile tissue of the hymenophore cannot be studied where there is no hymenophore and often likewise when there are merely veins. All species of Agaricales where a well developed hymenophore - tubular or lamellar - is lacking, are related to and often form transitions to forms with regular to irregular hymenophoral trama (see below). This heterogenous assemblage of groups of genera that have in the past been assembled with the old family Thelephoraceae sensu lato belongs in this category. In the Agaricales, we find this character exceptionally rather than constantly, except for a few genera that may well be interpreted as strongly reduced forms (some "Cyphellae", *Physalacria*). In others, we find mature hymenia of the same species, sometimes smooth, sometimes covering a lamellate hymenophore, or a venose hymenophore (*Geopetalum*, *Leptoglossum*, *Arrhenia*, *Marasmiellus*, *Marasmius*, *Mycena*, *Delicatula*). It must now be assumed that some species that were initially described or considered as *Helotium*, or *Cantharellus*, are actually Agaricales with either smooth, or venose hymenial surface. However, the so-called veins of such species as *Cantharellula umbonata* (*Cantharellus umbonatus*) or *Hygrophoropsis aurantiaca* (*Cantharellus aurantiacus*) are not true veins of the type encountered in *Cantharellus cibarius* but rather narrow lamellae with more obtuse edges.

In all but the exceptional cases mentioned above, and perhaps in *Geopetalum carbonarium* (A & S ex Fr.) Pat., the hymenophore of the Agaricales has either the shape of lamellae or of tubes. The examination of the internal structure of the hymenophore in these forms, i.e. the anatomy of the hymenophore minus the hymenium, is of great importance in taxonomy. The internal structure of the lamellae and tube walls is studied on longitudinal sections from the plane of attachment to the trama of the pileus down to the edge of the lamellae or the pore edges. In lamellate as well as in tubulose forms, care must be taken to cut exactly at a right angle to the edge of the lamellae\*, and exactly in the direction of the individual tubes rather than obliquely, i.e. in all cases, the section must be exactly vertical; it must also be exactly tangential, i.e. the lamellae should be sectioned at a

\*In ascendant lamellae as well as in the deeply decurrent part of the lamellae, the hyphae often do not run to the edge at a right angle (in relation to the latter), and in this case the section should be oblique in the sense of the direction of the hyphae of the hymenophoral trama since otherwise the proportions and shape of the hyphae and the structure of the hymenophoral trama may be misinterpreted.

right angle to their sides. It is also important that these sections are reasonably thin (about 15-20  $\mu\text{m}$ ) because otherwise pressure on the cover-glass has to be exercised in order to obtain a preparation transparent enough to show the arrangement of the single elements of the trama and adjacent layers. However, there is always a slight disorganization in such preparations, and if they are taken from old or otherwise poor material, the results will be unreliable. Under no circumstances may the preparations be crushed to the point where its elements are so dislocated that it is impossible to make an analysis of their arrangement. The beginner, and those who have to section material that is very scanty, brittle, or otherwise difficult to handle, and also those who find it difficult to learn sectioning by hand in the manner described above, are strongly advised to use a microtome. Both freezing and paraffin methods will do.

It is essential to keep in mind that the trama configuration may change during the individual development of a hymenophore. Particularly, the author (1945) has shown that bilateral trama may become seemingly regular or irregular in age, and that the taxonomic value of the configuration type of the hymenophoral trama resides in the young stages. As young stages we consider the stage just before or at the beginning of sporulation not, however, the primordium which, as Reijnders (1963) has shown, has often a bilateral-divergent arrangement of hyphae which becomes regular or irregular later, or on the contrary, at first regular, later bilateral (*Amanita*-type), or at first bilateral-divergent, then regular, and eventually inverse (*Pluteaceae*-type).

The sterile internal portion of the hymenophore consists of either one or several layers. If there is only one, it is called the hymenophoral trama\*. But more frequently, there are one or more equal layers on each side of the central hymenophoral trama, more or less easily discernible between the hymenophoral trama and the hymenium proper. If there is only one such layer, it is referred to as subhymenium, always consisting of small elements with numerous septa. If there is another layer between this and the hymenophoral trama, distinguishable from both the former and the latter in structure or characters of the elements composing it, it is called hymenopodium. In this book the notion hymenopodium is used in a wide sense and is defined rather by its position than by a uniform structure. This term may be restricted to its most commonly observed structure viz. a  $\pm$  narrow zone of thin parallel, sometimes gelatinized hyphae bordering the subhymenium. In this case, the subhymenium must be regarded as a remnant of the original generative hyphae after final differentiation of the hymenophoral trama. The hymenopodium in the more

\*Some authors use the word trama exclusively for the trama of the hymenophore. There is, however, no reason to reserve the term for only a single organ since the trama is not sharply delimited at the plane of attachment of the hymenophore to the pileus in the majority of the species. Only very rarely is there a differentiation between these layers (hymenophoral trama gelatinous, trama of the pileus nongelatinous in *Dictyopanus pusillus*), and even then, the trama of the hymenophore originates in the trama of the pileus. It is therefore more precise and generally preferable to specify as to the part of the trama considered. viz. the hymenophoral trama, etc. If the word trama is used alone, it should either be quite clear from the text or the arrangement that the hymenophoral trama is meant and none other, or else it must be supposed that whatever is said about the trama refers to all parts of the trama in the widest sense.

general sense should by no means be confused with parts of the hymenophoral trama proper, especially the lateral stratum of the bilateral hymenophore in an advanced state of maturity. More ontogenetical details may elucidate the true nature and origin of the zones between the hymenophoral trama proper and the subhymenium.

The hymenophoral trama occurs in four main types of structure:

1. intermixed to irregular (Pl. 27, 4),
2. subregular to regular (Pl. 27, 3),
3. bilateral (Pl. 25),
4. inverse (Pl. 26).

The difference between intermixed and irregular trama is secondary\*; both are characterized by completely or at least predominantly irregular arrangement of the hyphae which are neither parallel (not even approximately so) nor divergent. In the subregular trama and the regular trama, the hyphae run in approximately or strictly axial (from the plane of attachment to the pileus down to the edges of the hymenophore) direction, the hyphae being approximately axial although somewhat interwoven in subregular, more or less parallel in the regular trama.

In the bilateral trama, there is a central strand which is subregular or regular as described above but mostly thinner in diameter, sometimes reduced to a single tier or chain of hyphae, and an outer layer consisting of approximately parallel hyphae but which are not straight or parallel with the hyphae of the thin central strand but curve outward on both sides, joining the hymenopodium, or subhymenium, at a point farther outwards toward the edge of the pores or lamellae than the point at which each individual hyphae departed from the thin central strand. The thin central strand is called the mediostratum, and the divergent portion of the trama on both sides is called lateral stratum. The nature of the hyphae involved may be rather different. Sometimes, the hyphae of the mediostratum and the lateral stratum are of approximately the same type; but in other cases, the average diameter may be different in the hyphae of the mediostratum and the lateral stratum; the pigmentation may also be different, and the gelatinization, and consequently the density, the frequency of septation, etc. may differ in those two layers. Although it is true that it is mostly the hyphae of the fundamental tissue that are primarily responsible for the structure of the hymenophoral trama, in some cases, it appears that at least the more conspicuous part of the elements composing the trama and marking its arrangement is made up by the conducting elements; e.gr. in *Lindermycetes*, where the coscinoids (Pl. 30) diverge, almost without forming a distinct mediostratum, soon assuming a position perpendicular to the sides of the lamellae, thus making the hymenophoral trama very strongly (yet not typically) bilateral. There are also various types of bilaterality insofar as the relative density and diameter of the hyphae are concerned.

\*In the intermixed trama, we have elements of different shape and/or size mixed together, provided they do not run parallel with each other, in the irregular trama, all elements are of the filamentous type, with usually scattered oleiferous hyphae accompanying them.

The bilateral hymenophoral trama of *Catathelasma* consists of very thin hyphal elements whereas that of *Amanita* consists of rather broad and moderately long elements.

The structure of the hymenophore in these two genera is therefore not necessarily comparable although corresponding to the same basic configuration, viz. bilateral.

On the basis of Reijnders's work, there are two very different types of bilaterality, one which represents the early divergence of non-inflated hyphae and which he calls divergente (Josserand: épanouie; von Arx: truly bilateral), whereas in a different type of bilaterality the originally regular trama becomes bilateral because the hyphae, as they become inflated, gradually grow obliquely towards the exterior; they rise from the mediostratum. This second type is called bilateral by Reijnders (pseudobilateral by von Arx).

It would seem however, that the two types are connected by at least one intermediate subtype in which the trama of the primordium is at first bilateral, and later one observes in the mediostratum ramifications which become inflated and grow towards the exterior to form a bilateral trama much like that of the bilateral-pseudo-bilateral type.

It appears that hymenophoral trama structures are divided into certain types not according to the sequence of structures observed but according to the structure observed in young carpophores. The intermediate position of certain species with regard to the two types recognized by Reijnders and von Arx and, in addition, the different terminological conclusion to which these authors came, are arguments favorable to the solution accepted by me earlier, viz. to maintain the term bilateral in the original sense of Fayod (1889) and the French school of agaric anatomy, subdividing it, however, by recognizing an *Amanita*-type, a *Limacella*-type, a *Boletus*-type, and a *Phylloporus*-type (the latter two terms introduced and generally accepted since my early work on boletes).

The table I, p. 58 will illustrate the characteristics of each subtype.

In the family Tricholomataceae we have two types of tramal structure in the hymenophore: (1) Regular (sometimes subregular to almost irregular). (2) Bilateral. The subtype of bilaterality is here that of *Boletus* or *Phylloporus*. It is obvious that one is tempted to say that in this case the *Boletus* subtype of bilaterality is more primitive than the regular one since it is merely the expression of a longer maintenance of the divergent trama of the primordial stage. In this restricted sense I believe my earlier (1936) statement that bilaterality in Agaricales is a primitive character can be justified. It does not necessarily refer to the other types of bilaterality.

If the elements composing the hymenophoral trama differ from each other fundamentally, showing two main types of elements, thin, elongate, hyphal elements and swollen, voluminous, subisodiametric elements ("sphaerocysts"), the trama will logically be neither subregular nor regular; it will also not be bilateral unless the juxtaposition of these two types would coincide with what may be called a mediostratum and a lateral stratum. It is obviously a special case of an irregular trama,

Table I  
Subtypes of bilateral hymenophoral trama

Subtype	Primordial state	at beginning of sporulation	towards end of sporulation
<i>Amanita</i> -type	regular (illustration cf. Reijnders 1963, pl. 52 fig. 6)	hyphae inflate to clavate and diverge obliquely forwards in the lateral stratum (ill. cf. Bas 1969, fig. 15-16)	bilateral (ill. cf. Bas l.c.)
<i>Limacella</i> -type	divergent (slightly), (ill. see Reijnders l.c. 52, 4)	As <i>Amanita</i> -type	bilateral
<i>Phylloporus</i> -type	divergent	Still divergent, the lateral stratum scarcely looser than the mediostratum, hardly less colored, and only slightly more gelatinized, only slightly (but entirely) divergent, hyphae usually touching each other (ill. cf. Singer 1965 pl. 15, 2)	tending to become regular or subregular (hyphae becoming somewhat interwoven)
<i>Boletus</i> -type	divergent (ill. cf. Reijnders 1963, pl. 2, fig. 6)	Still divergent, the lateral stratum less pigmented, more strongly gelatinized than the mediostratum, its hyphae strongly curved outwards at first (ill. here pl. 25)	as in <i>Phylloporus</i> -type

and it is called intermixed trama, i.e. a trama where two types of elements are "mixed" with each other. Thus, the intermixed trama of the hymenophore should be interpreted as an extension of the heteromerous tramal structure into the hymenophore.

If the hymenophoral trama consists of a mediostratum and a lateral stratum, the latter consisting of hyphae curving outwards but reaching the subhymenium farther away from the gill edge rather than nearer to it as in the bilateral trama, we might assume with Fayod (who discovered this strange structure) that here the origin of the hymenophoral trama is in the subhymenium rather than vice versa. Perhaps, the isolated manner of development of the fundamental hyphae (here the hyphae of the lateral stratum), often observed in the trama of the carpophores of the Amanitaceae, manifests itself in the species with the kind of hymenophoral trama described above in that each subhymenial hyphal ramification produces either a hymenial element (on the outside), or an element of the fundamental tissue, more precisely the lateral stratum (on the inside). Reijnders (1963) observes that "soon the lamella-trama assumes a more regular aspect, sometimes also somewhat interwoven. In most cases, the subhymenium is immediately very broad; in *Volvariella bombycina*, for example, the mediostratum is immediately very thin... In this regular trama ramifications are produced which become soon inflated. These hyphae with rounded tip are at first more or less parallel with the hyphae of the

mediostratum; in a later phase, they deviate towards the middle where the characteristic inverse trama is produced, seemingly without mediostratum. Fayod as well as Walker (1919) believed that the inflated elements rise from the subhymenium; we have contested this point of view as well as the opinion according to which the hyphae are endocystidia ("cystides internes") although these hyphae seem, in fact, to rise from the subhymenium. But at times, one observes distinctly the rests of the mediostratum which has become completely separated and forms some kind of hymenopodium underneath the subhymenium. ...Evidently, this curious phenomenon... is a means of broadening the lamellae". Whatever its morphological and ontogenetical significance, this type of hymenophoral trama is of as great taxonomic importance as the other types, and has been named inverse trama (trama renversé, Fayod 1889). Good examples for intermixed trama are the *Russulae*; for irregular trama - *Pleurotus*; for subregular trama - *Hygrocybe* excepting the section *Conicae*; for regular trama - *Hygrocybe*, section *Conicae*; for bilateral trama among the boletes - *Boletus edulis* and all the other Boletaceae, among the agarics - *Amanita caesarea* and all the other species of *Amanita*; inverse trama - *Pluteus* (all species known), and related genera.

Less important differences in the structure of the hymenophoral trama can be distinguished as subtypes of the above basic types. These are:

1. *The Clitocybe subtype of the regular type*: The outermost hyphae of the otherwise regular hymenophoral trama show a very slight tendency to diverge but a mediostratum is not differentiated. Example: *Clitocybe dealbata*.
2. *The subcellular subtype of the regular type*: The elements of the otherwise regular trama are so grossly enlarged and broadened that the trama appears almost cellular at places. Examples: *Mycena*, *Psathyrella*, *Coprinus*.
3. *The Conocybe subtype of the regular type*: This differs from the preceding one by the fact, stated by Reijnders, that the primordial hymenophore is characterized by being for a long time remarkably thin and composed of parallel hyphae (regular) in *Conocybe pubescens*. However, there is no divergence of elements as in *Amanita*.

In certain genera of the Tricholomataceae (many *Resupinateae*, *Dictyopani*, etc.) and in some *Crepidoti*, the trama is partly or entirely more or less gelatinized. In *Panus*, *Pleurotus*, also in some species of *Marasmiellus*, in some *Xeromphalina*, *Anthracophyllum*, etc., the trama consists mainly of thick-walled, rather large, rigid, elongate hyphae, and in this type of trama, the thin-walled, thin, small, curved elements of the connective tissue are naturally more conspicuously different from the other elements which belong to the fundamental tissue. This difference may be expressed in calling this type of trama intermixed rather than irregular or subirregular, but it is obvious that this meaning of "intermixed" is not identical with what it is in *Russula* and should be discouraged.

In a few cases where the trama proper is strongly reduced in favor of a hymenopodium (rarely a subhymenium), the impression may prevail that the hymenophoral trama itself consists of two layers with the lateral stratum running exactly parallel with the mediostratum instead of diverging. This is the case in *Conocybe* (Pl. 26, 2).

In this case we may speak of false bilaterality. In Gomphidiaceae, e.gr. *Chroogomphus*, the hymenophoral trama is basically bilateral, yet the divergence of the lateral stratum is obscured by an increasing irregularity of structure as the carpophores mature while the mediostratum is so reduced that it is hardly recognizable especially in old specimens. It is consequently easy to mistake the broad hymenopodium that is not sharply delimited from the subhymenium, either for the lateral stratum of the hymenophoral trama, or for an unusually enlarged subhymenium.

This strong development of the hymenopodium is noticeable only in a minority of the Agaricales. The hymenopodium is completely irregular in those Agaricales with lamellate hymenophore but otherwise related to the boletes (Gomphidiaceae, Paxillaceae), and it is regular and consisting of broad, voluminous hyphae in *Conocybe*. It is also somewhat developed as a zone of more parallel and thinner hyphae bordering the subhymenium in some genera e.gr. *Russula*, *Mycena*, etc., where, however, its taxonomic significance, as far as can be seen now, remains at the species level. The hymenopodium is however of taxonomic importance where it is, in contrast to the mediostratum or the hymenophoral trama proper, gelatinized and composed of hyphae running along the subhymenium parallel to the mediostratum e.gr. in *Pholiota*. In a comparison with the bilateral trama of the *Boletus*-type, it might appear that the hymenopodium here is homologous with the lateral stratum of the hymenophoral trama of the Boletaceae, only that the hyphae in *Pholiota* are not divergent. It is indeed difficult to decide whether we have here a hymenopodium or a lateral stratum of the hymenophoral trama, although, by comparison with other Strophariaceae, one is inclined to think that the lateral stratum is not homologous with the hymenopodium. It is however obviously erroneous to speak of gelatinized subhymenium in cases like that of *Pholiota* section *Myxannulatae* (and other similar ones) since there is, aside from the hymenopodium, a differentiated subhymenium - gelatinized or not, consisting of a narrow layer of smaller, shorter elements directly underneath the bases of the basidia.

The subhymenium is rather uniform. It is rarely of great taxonomic importance with the exception of the genus *Pleurotus* (Pl. 26, 4) where it is well developed in contrast to *Panus* (Pl. 23, 1) where it is very narrow to almost absent, and *Leucopaxillus* where it is filamentous (ramose), whereas in *Armillaria* it is cellular. This latter difference is not always so sharp as in the case of *Armillaria* and *Leucopaxillus*. This can be seen in some species of *Gomphidius* where the crowded septa shorten the individual cells so much that the whole seems to be a minutely pseudoparenchymatic tissue. Wherever the septa are not so close, the subhymenium assumes a more filamentous character. Wherever the elements become irregular in shape and denser and more intricately interwoven, we have an intermixed subhymenium, as is the case in *Chroogomphus*, or *Gerronema*, subgenus *Romagnesia*, or some species of *Resupinatus*.

In these species of *Resupinatus*, the trama proper of the lamellae is gelatinized, looser and more regular. In other groups, especially the section *Laetae* of the genus *Hygrocybe*, the hymenophoral trama is nongelatinized while the hymenopodium or subhymenium is strongly gelatinized. This is one of the very few cases where the large diameter and strong differentiation of the subhymenium may lead to the

misinterpretation as though the trama proper were bilateral whereas, actually, here again we have an example of false bilaterality. The size, shape and structure of the subhymenium is also used taxonomically in the characterization of some sections of the genus *Lactocollybia* (Tricholomataceae).

In genera with regular trama, the subhymenium is often separable from the hymenophoral trama, and then the lamellae are macroscopically described as fissile, a feature frequently found in agarics but hardly of much taxonomic value.

The subhymenium usually accompanies the hymenium all through the interlamellar zones at the top of the interlamellar space, and in certain cases, the hymenophoral trama or its parts run parallel with it. In this case, a looser layer of differently organized hyphae separates the hymenophore from the trama of the pileus. As a consequence, the hymenophore can be easily separated from the context of the pileus. This is especially remarkable in Boletineae where the hymenophoral trama is bilateral and forks above the level of attachment of the hymenophore to the trama of the pileus - thus facilitating the separation of the tube walls or lamellae together with the ceiling of the tubes or the interlamellar zones. The separability of the hymenophore is however not restricted to the Boletineae but its taxonomic significance has been exaggerated by the early mycologists in such genera as *Lyophyllum*, *Lepista*, and others.

Certain agarics possess a special epiphyllous or supralamellar zone of a structure different from that of the trama of the pileus as well as the trama of the hymenophore. This may also result in an increased separability of the hymenophore as a whole.

The structure of the hymenophoral trama has at present become one of the most important characters in the Agaricales. Tribes, genera, even families are based on the structure of the hymenophoral trama wherever this character is correlated with other important features. There can now be no methodical analysis of any representative of the Agaricales without a careful study of this particular character.

## XVI. CORTICAL LAYERS

Cortical layers are formed by a differentiated tissue forming the surface layer of the pileus and stipe of the Agaricales. We have already seen (p. 44) that cystidioid bodies, reminiscent of those that occur in the hymenium either on the sides of the lamellae or in the interior of the tubes - or on the pore or lamella-edges, are also found in the cortical layers as relics of an originally indiscriminately expanded hymenium, or as products of a further differentiation of the cortical layers whereby they may have assumed some specific function. The cases where these cystidia are remainders of a primordial hymenium are not rare in the Boletaceae, e.g. *Suillus*, sect. *Granulati* (Pl. 76, 8, 9); the reticulate *Boleti*, and *Tylopili*, all species of *Leccinum* (Pl. 40), and the alveolate species of *Austroboletus* and *Boletellus*. Here, the ornamentation of the stipe is still reminiscent of the configuration of the hymenophore. In many of these, even sporulating basidia are found among sterile bodies

making up the palisade of the cortical layer covering these ornamentations, especially in the upper portion of the stipe. In rare cases even the whole marginal zone of the pileus is covered by a hymenium, a large portion of which consists of basidia (Pl. 77, 5, 40). All this is proof enough that these bodies are of hymenial origin. It is very difficult to state in every single case, whether the elements of the cortical layers are of hymenial origin, or later acquisitions due to an increasing differentiation and division of functions. It is not even certain that, if these elements should have been differentiated in a later stage of the evolutionary development of a genus, they cannot have originated from the hymenium or an extension of it. In such cases as *Russula mariae* where we find the same type of elements on the edge of the lamellae and on the cortical layers, it may well be that they are both modifications of a degenerated hymenial element.

Considering all this, it does not seem possible at present to distinguish between such cystidoid bodies that have a non-hymenial origin and such that evidently originate from hymenial elements. Consequently, it is, in the author's opinion, correct to refer to all cystidoid bodies of the cortical layer as cystidia or pseudocystidia, if they are in some way comparable with either cystidia or pseudocystidia of the hymenophoral hymenium, with the only difference that those bodies that occur in the cortical layers receive the prefix *dermato*\*. Thus, we have, in the cortical layers:

1, dermatocystidia (Pl. 40; 58, 1dc; 65 4dcy; 66, 6dcy, 7pc, cc, 8dep, dcs; 70d; 76, 9; 77, 5; 79, dc; 80, 2; 82 st); 2, dermatopseudocystidia (Pl. 39).

Although it is not yet customary to refer to "dermatogloeocystidia" or "dermatocystidiolae"\*\* or "dermatometuloids" or "dermatochrysocystidia" or "dermatomacrocystidia", etc. (all these bodies are being called dermatopseudocystidia, or dermatocystidia) it is correct to call the basidia occurring on the stipe or the pileus, outside the area covered by the hymenophoral formations, dermatobasidia, and those of them that remain permanently sterile with slight modifications in size or shape, but strongly differ from the cystidia, - dermatopseudoparaphyses.

Dermatobasidia are found on the pileus of *Boletus subsolitarius* and many *Russulæ*, and much more commonly on the apices of the stipes of the boletes and agarics. If fertile dermatobasidia occur in a hymenium-like structure on the surface of the pileus or the stipe, we may then refer to that structure as to an extension of the hymenophoral hymenium, and call it extrahymenophoral hymenium. If there is a hymenium-like structure outside the hymenophore that lacks dermatobasidia and, for that matter, also dermatopseudoparaphyses, we call this structure - hymeniform, and the layer, made up by it, a hymeniform layer (Pl. 32).

If the cortical layer is formed by septate hyphae, inserted more or less perpendicularly to the surface of the organ in question or ascending gradually yet not being strictly hymeniform, it is called trichodermium (Lohwag 1937, 1941; Pl. 71, 1); if

\*As for the prefix pilo- and caulo-, see p. 111.

\*\*Naturally, with a subhymenium in the proper sense being absent in the cortical layers, it would be difficult to state whether a dermatocystidium has cystidiolae character or not.

the trichodermium is gelatinized as in *Suillus granulatus*, it is an ixotrichodermium (Snell, in Elrod & Blanchard 1939). These hyphae usually form a velutinous to tomentose surface, but at times, especially when densely interwoven, they are not easily recognizable macroscopically; in the ixotrichodermia, the surfaces covered by it are, as a rule, merely glutinous. If the hyphae are vertical (erect) and parallel with each other, we speak of a trichodermial palisade (Lohwag 1937, 1941) which differs from the hymeniform layer in that not necessarily every element originates and ends at the same level as the neighboring elements of the same nature\*. Trichodermial palisades (Pl. 27, 1; 34; 70e, 77, 1, 8; 78, 2, 3, 4) usually make the surfaces they cover velutinous, or granulose, or pruinose; they never present, macroscopically, a watery, smooth or a coarsely tomentose aspect. The rimose or rimulose surface (as in contrast with the rivulose surface) in many boletes is a result of this kind of structure, that easily lends itself to perpendicular cracks that spread tangentially in all directions. Trichodermial palisades are also common in the Agaricaceae. The terminal members of the hyphae forming trichodermial palisades frequently are cystidioid, i.e. they are dermatocystidia, probably in most cases of the leptocystidia- and cystidiole-type (example: *Phaeomarasmius*).

If the trichodermium, especially the trichodermial palisade, consists of shortened hyphal elements that tend to become sphaerocysts (isodiametric cells), the result is a mass of subglobose or globose bodies - with or without showing the original catenulate arrangement - that can be characterized as a loose pseudoparenchymatic layer. This type of cortical layer is called epithelium (Lohwag 1937, 1941), or a cellular layer (Pl. 35, 77, 7). If there is only one stratum of sphaerocysts which are, with their base, directly attached to the hyphae of a lower layer, it is often impossible to differentiate between a hymeniform layer and an epithelium inasmuch as some of the sphaerocysts of the epithelium are often mucronate at the distal end or slightly vertically elongated (short-ellipsoid or short-clavate). The pluristratous epithelium is closer to the trichodermial palisade, especially in such cases where short and long hyphal members alternate, or the shape of the single elements of the chains change from one chain to the other, or in individual carpophores (Pl. 77, 3). In many cases the elements of an epithelium show a tendency to become an accumulation of isolated sphaerocysts or other short cells and this leads to pulverulent strata which often adhere to the finger or needle (they are "detersile") as in the volval covering of the pilei and stipes of some Amanitas, *Phaeomarasmi*, *Coprini*, in *Psathyrella kellermanii* and some Mycenes of section *Sacchariferae* as well as in the genus *Cystolepiota* and other Agaricaceae such as *Phaeolepiota*.

In some of these examples, we can observe single cells becoming separated from the neighboring cells. This is also the case in some Myceneae (Tricholomataceae) where the terminal cells become isolated bodies (a furfuraceous covering or a pruina) which may be interpreted as a velar layer. In this layer the cells becoming isolated are often characteristically thick-walled and diverticulate to spinose and are then

\*According to these definitions, the hymeniform layer is a special case of trichodermial palisade.

called cherocytes\*. Such bodies are found in some species of section *Basipedes* of *Mycena* and in *Amparoina*.

If the cortical layer is formed of radially arranged or, at any event, repent hyphae that are parallel to each other, it is called cutis (Lohwag 1937, 1941) (Pl. 38, 68 A 7). In some genera the cutis forming the cortical layer of the pileus is a constant feature and for purposes of infrageneric taxonomy can be divided into two types (1) with the hyphae rather broad, all repent or only with scattered and not differentiated vertical or ascendant side branches - not running parallel with each other on any given level and not radially arranged, often branched although not coralloid-diverticulate: The *Dryophila*-type (well developed in *Collybia dryophila*) and (2) with the hyphae rarely branching and running radially from the disc to the margin of a centrally stipitate pileus or from the rear to the margin of a fan- or shellshaped pileus: The *Confluens*-type (well developed in *Collybia confluens*). The hyphae of the cutis may also be gelatinized, i.e. imbedded in a gelatinous layer and in this case we speak of an ixocutis.

Typical *Asterostromella*-structure such as described for the genus *Vararia* (Aphyllophorales), is not found in the Agaricales; however, a structure reminding one of although not fully identical with the *Asterostromella*-structure (or, for that matter, of the structure of *Lachnocladium brasiliense*) - and in Agaricales always restricted to a single layer (usually the cuticle of the pileus), does occur and is called asterostromelloid or dichophysoid structure. This structure is found in *Resupinatus*, and to a lesser degree in *Campanella*. It is characterized by hyphae with short branches and secondary, etc. ramifications, all branching off under approximately right angle and at short distances, frequently causing a stellate appearance of the terminal hyphae. These elements are rather stiff, and more or less hyaline (pl. 36). This structure should not be confused with a structure characterized by diverticulate hyphae as in many Mycenes, nor with an irregular system of branching (not simply repent) diverticulate, nodose, appendiculate and forked to coralloid hyphal elements such as found in *Marasmiellus*, especially sect. *Rameales*, and therefore referred to as *Rameales*-structure (Pl. 57D, above; 58, 2ep). But this structure is not confined to the Marasmielli and related genera; it is also found in *Coprinus* section *Alachuani*. In both these cases the resulting structure differs from asterostromelloid structure in either simple (once diverticulate) not repeatedly ramified hyphae, or in a less regularly branched system. In *Campanella*, and *Resupinatus* transitions from asterostromelloid to *Rameales*-structure can be observed.

In numerous species the cortical layer is not or only slightly developed. In some *Russulae*, a dense, turf-like covering of normal, very thin hyphae which are often forking or branching, reach the uppermost layer of the cuticle. They are not always enough organized to be called ixotrichodermium or trichodermium. A similar, still less differentiated layer is found in the cuticle of some species of *Crepidotus*. In other species, such as *Panus conchatus*, the cuticular layer is merely denser (as that of the stipe is often denser in a "rind") than the trama of the pileus. Such a

\*Originally named acanthocytes (Singer 1983) but this term has been used earlier by Farr (1980, see chapter II. p. 4).

structure is very frequent in the Agaricales, especially in the white-spored families, and cortical layers of this type are called "dense" (Loquin's "cortex", a term too ambiguous to be of much help in this instance).

It should always be taken into consideration that certain types of veil (most conspicuously so the volva of *Amanita*; Pl. 33, 1), leave a layer of fragments of not truly cortical origin on top of the cortical layers. When an analysis is made, care should be taken that these velar layers are not misinterpreted as being part of the cuticle. Such precaution can easily be taken by examining the structure of the veil first and subtracting any layer of identical structure and origin from the layers of the cuticle proper.

The cortical tissue itself consists of one to three layers. If there is only one, we simply call it cuticle\* of the pileus (pellicle - if it is viscid, and peels easily), and the covering layer on the stipe. If there are more than one the uppermost layer in a completely developed specimen\*\* is called epicutis. The epicutis may be a continuous layer in one of the types of structure named above (hymenium, hymeniform layer, trichodermium, epithelium, cutis, dichophysoid layer, or dense layer), or else it may consist of fragments of such a layer. In this case, the epicutis is the sum of dissociated but identical individual dermatocystidia, dermatopseudocystidia, "hairs", or any other type of bodies characteristic for this particular layer, and its origin in this case must be understood as conditioned by the rapid growth of an elastic supporting cuticular layer while the epicutis layer stops developing at an early age. Such cases are not rare in the Agaricales, especially in such groups where the epicutis is the remainder of an early extension of the hymenium beyond the hymenophore, such as the epicutis of the Russulaceae (pl. 38), or at least many species of that family.

The epicutis is followed, downwards, or rather inwards, by a second layer, the hypodermium or subcutis. Though it seems illogical, general custom applied the term hypodermium, as a general term, for any structure between the epicutis and the context in most Agaricales (Fayod 1889). In the species that have a cutis, the term subcutis is preferred by Lohwag (1937). Subcutis thus would become synonymous with hypodermium unless the term is amended to be any layer underneath the epicutis but confined to the cases where the cuticle consists of three layers, and then the upper layer (intermediate between the epicutis and hypodermium) is called subcutis, e.gr. in *Russula puiggarii* where, underneath a well-developed epicutis, a layer of hyaline gelatinized hyphae is followed, farther downwards, by a layer of pigmented, non-gelatinized hyphae. In the author's opinion, the term subcutis should not be used in preference to the term hypodermium for any single (or supposedly single, i.e. considered as one by the observer) layer between the epicutis and the context of the pileus or stipe.

\*If this single layer can be shown to be homologous with one of the three cuticular layers in related forms, for example with the epicutis, it is also proper to call it so.

\*\*In *Agrocybe* and some other genera, the uppermost layer is somewhat detersile, and often washed off by rain or handling. It is therefore quite frequently missing in old or carelessly prepared specimens; on the other hand, it is not yet clearly differentiated in the primordium.

Lohwag in his original proposal (in Lohwag & Peringer 1937) did not pay attention to the fact that he was dealing with two different categories: structure of layers, and sequence of layers. If the subcutis is understood in a revised sense, valid only for the naming of a layer in a certain position, and not descriptive of its structure, the short cells immediately beneath the "hairs" or dermatocystidia of species with *Virescens*-structure (see below), or of species with trichodermial palisade (as *Porphyrellus pseudoscaber*) might be called subcutis\* (Pl. 33).

Another layer that does not necessarily belong to the cortical tissue, must be mentioned here. In some species of Agaricales, one can observe a layer of the context of the pileus that is differentiated from the rest of the context not morphologically but merely chemically or physically, i.e. it does not show the difference between the rest of the trama and itself unless it is exposed to a certain kind of radiation, or to certain reagents. This layer has been termed the subhypodermial layer of the context (Singer 1942), in a discussion of the physical and chemical differentiation of this zone in certain species of the Gomphidiaceae. As another example, one may indicate the pigmented upper zone of the flesh of *Mycena amygdalina*. Yet, here it may be questionable whether the pigmentation is a purely chemical or physical character, inasmuch as it is not provoked by any chemical reaction other than the normal chemism of the developing carpophores in nature. It will nevertheless be expedient, though perhaps on a temporary basis, to maintain the term subhypodermial layer for a case like that of *Mycena amygdalina*. The same term may also be used for the zones of the context of the *Paneliae*, *Resupinati* and *Crepidoti* that are or become gelatinized.

Gelatinizing of the hyphal walls whereby the hyphae become imbedded in a mucous mass - given enough moisture - is observed very frequently in the main cortical layers of the Agaricales, and the macroscopic consequence of such a condition is what is generally called a viscid or glutinous surface (pileus or stipe, or both). If such is the case, the cuticle is often called pellicle because of the easiness with which it can be peeled from the non-gelatinous (or less gelatinous) layer. It must be kept in mind, however, that the separability (the peeling quality) may also hold for a non-gelatinous cuticle that is separated from the lower layers of the trama by a gelatinous subhypodermial layer. The hyphal walls often gelatinize so completely that the walls practically disappear whereby the gluten becomes macroscopically homogeneous. Without the coherence due to the presence of the hyphae, the gluten often drops down, or is washed down, and the anatomical demonstration of such a specimen as having been glutinous or having had a gelatinous layer on or near the surfaces becomes very difficult or impossible. This is apparently the case in certain species of *Hygrocybe*, especially if herbarium material is examined.

A chemical difference between cuticular layers on one hand, and tramal layers of the context on the other hand, is often demonstrated by the iodine stain. This

\*The subcutis would then, in many cases apparently, be homologous with the subhymenium of the hymenophore. It might be inferred from what Lohwag & Peringer say about Fayod's term "cuticule proprement dite" that the latter was identical with what we call subcutis. This, however, is not the case since Fayod calls by this name either the epicutis or the hypodermium whichever is more developed.

feature will be treated more exhaustively in chapter XIX on chemical characters.

In the discussion of the layers and elements observed in the cortical tissue of the Agaricales, we have not used the word hair so extensively as it is used by some authors. This word, when used as a term, mainly for differentiated terminal formations of hyphae in the epicutis, can often be replaced by the term dermatocystidia, or the more neutral expression "epicuticular elements". However, if these elements actually resemble hairs - there is no objection to calling them hair-like hyphal ends (Pl. 41; 56 st; 61 st; 63, 1 a-f, 4 b, i; 65, 4 h; 66, 6 h), and if the "hair" is actually a strand of hyphae, it may be called a hairlike hyphal strand (Pl. 36), or a pilose agglutination of hyphae, all neutral expressions. The author accepts the term hair only for those epicuticular elements that are hair-shaped, form a pilose covering or velvet under a lens and are not homologous with cystidia, cheilocystidia, pseudoparaphyses, or setae, or any other well-defined bodies. Such true hairs are found in all species of *Flagelloscypha*, *Lachnella*, *Crinipellis*, *Chaetocalathus*, and in some species of *Coprinus*, *Pseudohiatula*, *Mycenella*, and the covering that is made up by them is called pilose.

However, if the "hair" is much rather comparable to bodies that, as cystidia or cheilocystidia, or pseudocystidia, also occur in the hymenium of the hymenophore (even if the bodies occurring in the cortical tissue are slightly modified or if the corresponding body in the hymenophoral hymenium is absent in a given species, yet present in a closely allied form), the use of the word dermatocystidium recommends itself much more than the indiscriminate use of the word "hair". For all these so-called "hairs" the term can only be applied in the case that Romagnesi's (1944) thesis is accepted which differentiates between cystidial and pilose elements in a manner that is at variance with that adopted in the present book\*.

This also refers to the characteristic cells with apical appendages (giving them a broom-like appearance) occurring on the pileus and sometimes on the edge of the lamellae in *Marasmius*, sect. *Sicci* and *Hygrometrici* and some other sections. The sterigma-like appendages ("setulae") and the palisadic arrangement as well as their occurrence on the edges of the lamellae in some species may suggest a hymenial origin, and this is also the author's guess. Since there is a good term in French literature (cellules en brosse) which can be adapted to other languages, we designate these bodies as broom-cells in a category by themselves at least for the time being (Pl. 31; 54 epi; 62, 9 epi, 10 epi). Broom-cells may form a hymeniform layer or, more rarely, not and then there are all kinds of transitions from broom-cells to *Rameales*-structure (e.g. in *Marasmius* sect. *Androsacei*).

In *Russula vesca* and species with similar elements in the epicutis, we find an elongate erect epicuticular element in palisade that by Maire, Singer, Melzer & Zvára, Romagnesi, and other specialists has been referred to as "hairs". It consists of a few basal cells which are rather short-cylindric to sphaerocystoid, and the terminal member which is attenuate toward an obtuse or acute tip from a broader

\* "The cystidium ... is a sterile cell ... characteristic for the basidia-bearing part of the hymenium". "The hair ["poil"] is a sterile cell ... which is originally characteristic for the covering layers ["revêtements"]". Romagnesi, *Rev. Myc.* 9(1): 6. 1944.

basis. More rarely a small appendage, which is usually more or less cylindric, is separated from the elongated cell by a septum. With *Russula modesta* as an intermediate, this structure of the epicutis goes back to the so-called *Virescens*-structure found in *Russula virescens*, *R. crustosa*, *R. patouillardii*, *R. chlorinosma*, and the entire section *Plinthogali* of *Lactarius* (Pl. 33, 87). Here, the basal cells are more conspicuous, truly made up by erect chains of sphaerocysts, and ending up with a subulate or cylindric, rarely clavate or ventricose "hair". In both the case of *Russula vesca* as well as in that of the *Virescens*-structure it is probable that the "hairs" are merely modification of a transformation of some originally hymenial body. In fact, the acute cheilocystidia of some of these species are not basically different from the "hairs", and the short cells from which the latter originate can be compared with the subhymenial elements from which the cheilocystidia originate. Since the edge of the lamellae is not quite sterile, it is not difficult to see that these cheilocystidia have the same origin as the basidia. They gradually turn, however, into macrocystidia, since, for instance in *Russula crustosa*, already near the edge and on the edge many of the cheilocystidia have contents that turn blue in sulfovanillin, and farther upwards on the sides of the lamellae they become very voluminous and deep-rooted true macrocystidia. Since we have a situation similar to that in *Marasmius* with its broom-cells, it is necessary to provide a new term for these bodies, i.e. the terminal "hair" in the *Virescens*-structure as well as the "hair" in the epicutis of *Russula vesca*. This is necessary inasmuch as the use of the plain term dermatocystidia (which would otherwise be correct) may lend itself to confusion with what was formerly called dermatocystidium in the Russulaceae, i.e. the dermatopseudocystidium of macrocystidial or perhaps sometimes gloecystidial origin. The "hairs" in the Russulaceae will therefore be called ciliate dermatocystidia in this book, a term that does justice to the homology established by Maire as well as to the rather descriptive name of these bodies, suggested by J. Schäffer (Wimpern, Cilien).

There is another term in *Russula* that must be mentioned here. In the velutinous and flocculose species, the hyphae forming the trichodermium or the trichodermial palisade, are often thickened, as compared with the narrow elements of the connective tissue, quite frequently multi-septate, yet, the single elements still remaining elongate and usually cylindric; they are incrusted, rarely seeming naked, slightly acuminate but rounded, or broadly rounded at the ends; they are colored (usually pale ochraceous). Melzer & Zvára (1937) called these "hairs" in Czech "vlákna primordiální" or "hyfy", Singer (1932) in German "Flockenhaare". Melzer and Singer agreed later to the term primordial hyphae which Melzer claims is used in the sense of Fayod. These primordial hyphae were later (misleadingly) renamed "Haare" (hairs) or "Fasern" (fibrils) by J. Schäffer (1934). Romagnesi (1967) showed that the often elusive incrustation of primordial hyphae is best demonstrated by Melzer's own procedure: coloration with basic fuchsin, and after acidification of the medium with diluted hydrochloric acid, observation in water.

All these bodies in the Russulaceae can be distinguished according to shape and, to a certain degree, origin. However, here again, we find so-called transitions already noticed by R. Maire (1907 and 1910) in which elements that morphologically seem to

belong to one type of epicutis bodies differ chemically, i.e. acquire macrocystidial character. This becomes a specific character in *Russula peckii* where all so-called "hairs", i.e. the ciliate dermatocystidia reveal bluing granules when treated with sulfovanilline. It would be, in the author's opinion, proper and descriptive to call this ambiguous organ "ciliate dermatopseudocystidia"\*\*.

A good attempt to combine both the position and the structure of cortical layers into a new set of terms was made by Locquin (1953) whose scheme has not been accepted more widely because too many and too long-winded terms had to be coined and because the great variety of combinations actually found in Agaricales would make it necessary to increase the number of terms almost *ad infinitum*.

For the benefit of those who have no experience with the use of all the terms applied to the cuticle and its elements, it must be emphasized that in enumerating and defining them, we are dealing with three categories and these categories should always be understood and clearly distinguished as such:

1. *Layers without regard to structure*: Velar layer, cuticle (pellicle); epicutis, below it the subcutis, below it the hypodermium, below it the subhypodermial layer.
2. *Structures of layers*: Hymenium (mostly in epicutis), or hymeniform layer; trichodermium, trichodermial palisade; ixotrichodermium; epithelium; dichophysoid structure; dense structure; asterostromelloid and *Rameales*-structure; cutis of smooth or of simple divericulate hyphae.
3. *Elements of these layers*: Dermatocystidia, ciliate dermatocystidia, dermatopseudocystidia, ciliate dermatopseudocystidia, dermatopseudoparaphyses, dermatobasidia, differentiated hyphal ends, broom-cells, hyphae of the fundamental tissue, hyphae of the connective tissue, dichophysoid hyphae, primordial hyphae, sphaerocysts, hairs, structure-less mucilaginous masses.

## XVII. SPORES

### *Asexual spores*

In the Agaricales, uni-nucleate and binucleate oidia, conidia, and chlamydospores are comparatively less common than in some other orders of fungi although in culture under definite culture conditions and on definite media, arthrospores (oidia) are observed relatively frequently. The chlamydospores of *Asterophora* and *Squamaria* have taxonomic importance as a generic character whereas the presence of conidia in other groups has ordinarily not more than the value of an auxiliary specific character inasmuch as the conditions under which conidia are formed in nature, their constance, and even their existence in many species are unknown (see Brefeld, Vandendries and others on *Coprinus*).

\*These facts, taken from the anatomy of the Russulaceae, are especially instructive because of the thorough study that has been devoted to them by several authors whereby the knowledge of the anatomy of the Russulaceae was temporarily extended beyond our general knowledge in the Agaricales.

In *Asterophora*, the chlamydospores (Pl. 11) arise from the binucleate phase of the fungus, more precisely from the upper portion of the pileus or the hymenophore and also from the binucleate mycelial hyphae. These portions of the fungus become pulverulent, and, at the same time, the hymenophore and the production of basidiospores appears to be suppressed to a certain degree. However, basidia and basidial spores are formed in both the known species, and they have even been brought to germination by Brefeld (1889). The resulting mycelia often disintegrate into oidia chains. The chlamydospores can also be obtained in culture; they are formed predominantly intercalarily in *A. parasitica* where they are smooth, and predominantly terminally in *A. lycoperdoides* where they are coarsely stellate-echinate; the chlamydospores have been observed to germinate by various authors, and even carpophores have been obtained in culture (Thompson 1936). It is now amusing to look back at the classical controversy between those who attributed the chlamydospores to the agaric and those who wanted to see in them an ever-present parasitic Fungus Imperfectus.

Aside from *Asterophora*, some species of *Pleurotus* produce chlamydospores on special coremium-like carpophores which are comparable to arthrosporocarps but, instead of arthrospores, produce chlamydospores. These imperfect fruiting bodies may be called "synnematoid carpophores" (see p. 19). Chlamydospores are also formed on protocarpic tubers (see Bas 1965, Singer & Cléménçon 1973, and chapter VIII). The cherocytes ("acanthocytes") of *Mycena* and *Amparoina* may also be interpreted as chlamydospores.

As for the arthrospores of *Nothoclavulina ditopa*, see p. 18, 264.

### *Basidiospore formation*

The main form of propagation in the Agaricales is by the way of anemochoric basidiospores\* which are formed by the basidia of the hymenophoral hymenium; a small minority in a few species is formed by dermatobasidia and these spores are, in all cases investigated thus far, identical in all respects with the spores formed by the basidia of the hymenophoral hymenia. The hymenia sporulate throughout the mature life of the carpophore in the fleshy forms but are frequently found in a non-sporulating stage (inaccurately, these carpophores are usually referred to as sterile). This is much like the conditions in the tough and leathery Aphyllophorales, especially the *Microporus-Daedalea* group (Coriolaceae) and the Stereaceae. These long-lived (though in the Agaricales always annual) carpophores "time" the sporulation period or periods in accordance with the weather conditions and the seasons. For the practical purposes of spore study, the genera of the Polyporaceae, the genus *Trogia*, and the genera *Collybia*, *Marasmiellus*, *Marasmius*, *Crinipellis*, *Chaetocalathus* and related reduced forms are most annoying. Otherwise, the spores are always present in larger or smaller numbers though often not in sufficient quan-

\*In papers on Agaricales, the word spores customarily refers to the basidiospores; the latter word, a more exact term, is rarely used.

tity to produce a spore print. The examination of the spores from spore prints is preferable to the examination of the spores found in fragments or sections of the hymenophore. The spore print contains mainly mature spores and in a preparation taken from a print it will not be necessary to fall into the habit of measuring only the largest spores (as was done by Bresadola) in order to be sure to exclude immature spores, and also of measuring all spores, excluding the very smallest and the very largest (as was done by Lange). These methods will invariably, in an average, yield too large, or too small measurements which can be demonstrated if the measurements obtained by these methods are compared with those obtained by measuring all sizes of spores from a spore print\*. Not only the measurements will be exact, it will also make it impossible to create *nomina ambigua* by studying the hyphae of one species and the spores of another as has sometimes happened when a large amount of foreign spores (even mould spores - *incredibile dictu*) was blown on the hymenophore of the specimen under examination while it was in the basket or in situ.

### *Shape of basidiospores*

In shape, the basidiospores vary from almost perfectly globose (Pl. 14, 1; 84) to strongly elongated, from round to nodose (Pl. 17), stellate, cross-shaped, or angular (Pl. 12, 1; 16; 53 A; 72, 5-6) in circumference, and from terete to laterally compressed (Pl. 13; 73, 3) or angular (polyedric) when seen from one end (the longitudinal axis toward the objective of the microscope) (Pl. 10; 75, 8-9). They are rarely perfectly orthotropic (Corda 1842) and equilateral, a feature common to almost all spores produced on the outer surface of carpophores in the Basidiomycetes, and often put in contrast to the symmetry of spores produced by "angiocarpous" (endocarpic) forms. This can be explained by the manner in which the spores are produced and discharged at the tip of the sterigmata. A study of the spore discharge in non-angiocarpous Basidiomycetes shows that the inaequilateral spore is advantageous in spore discharge, or at least a logical byproduct of the exogenous discharge\*\* whereas in angiocarpous Basidiomycetes, the spores are disseminated through a final disintegration (partial or entire) of the peridium, or by other devices, after the basidia themselves have collapsed and disappeared in the gleba. The spores are consequently freed from the sterigmata by the disintegration of the basidia rather than by forceful discharge, and they are not in need of any lever action or any other advantage gained by the asymmetry (or heterotropism, Corda 1842) of the spores so general in the non-endocarpous forms. While all this is obviously basically true, the further statement that, therefore, all Agaricales have heterotropic spores,

\*R. Maire also enumerates other sources of error in spore measuring (comparison of measurements in different media, faulty use of the ocular micrometer, etc.) in a paper that will be very helpful for those in need of more elementary advice in techniques (*Bull. Soc. Myc. Fr.* 42: 43-50. 1926).

\*\*See the various theories given on spore discharge in Basidiomycetes by Buller (1924), Ingold (1939), Lohwag (1941), Prince (1943), Corner (1948), McLaughlin (1982). It appears that the mechanism (septation, etc.) varies in the different groups.

and all *Gastromycetes* orthotropic spores is not a law without exceptions. In the first place, the spores of most *Gastromycetes* (the author has studied in this regard all "secotiaceous" genera and *Torrendia*) are not all perfectly orthotropic, but some spores are usually heterotrophic because of the lower or more oblique position of the sterigma on which they were produced. Furthermore, the so-called gastroid form of *Boletinus decipiens* which, biologically speaking, is a *Gastromycete* rather than a bolete, has truly heterotrophic spores. Some *Russulaceae* that are otherwise close to certain *Gastromycetes* of the group called *Astrogastraceae* by French authors, and form their spores either gymnocarpously or pseudoangiocarpously, have spores so close to truly globose that it is very difficult to establish whether they are inaequilateral while still being slightly obliquely attached by their hilar appendage which makes for a certain degree of heterotropism. This "almost orthotropic" manner of spore formation cannot otherwise be explained than by the assumption of close affinity of these species with true *Gastromycetes*. Orthotropism and heterotropism of basidiospores are, consequently, not a character of immediate adaptation to either endocarpic development of the carpophores or to non-angiocarpous spore production, even though, historically and evolutionally, the manner of development appears to be the source of this divergence of spore development.

In the second place, as we have already seen (p. 41), the autobasidium produces at least two types of sterigma-spore configuration (Singer & Grinling 1967) even though the type commonly described (Malençon 1931) is by far the more frequent one.

As I have shown in *Omphalotus olearius* and *Gerronema venustissimum* sterigmata of 1-spored basidia have a tendency to be elongated and often suppress spore formation; they are filiform (not half-sickle-shaped) and often widened into an aborted spore-like tip or they may grow out into simple hyphae. This is also found in 2-spored and 4-spored basidia, for example in *Neoclitocybe latispora*. Another example was described by Heim (1970) in an unidentified hygrophoraceous species. We have here a first step towards suppression of the basidiospore and direct germination of the basidium.

The strong inaequilaterality of the spores of many *Agaricales* makes it easier to differentiate between an inner or "adaxial" (Corner) - often flatter or even depressed - and an outer or "abaxial" (Corner) - often more ventricose - side of the spore; in elongate spores these sides are distinguishable (see e.gr. pl. 76, 11) to the right and left of the longer axis. The hilar end (base) of the spores is oblique and the hilar appendage (part of the spore that joins the tip of the sterigma, also called "apiculus" or "sterigmatal appendage" by purists) is nearer the inner side than the outer side. It lies in the direction of the geometric axis of the spore only if seen not in profile but from the adaxial or abaxial, i.e. from the inner or the outer side. If the spore is turned around the geometric axis by 90°, i.e. when seen in profile, the hilum becomes somewhat removed from the geometric axis. On the other hand, the apex of the spore is always on the distal end of the geometric axis of the spore\*. In spite

\*This is one safe way, for the beginner, to make sure which end of the spore is the apical, and which the basal end when the spore is detached from the basidium.

of its inaequilaterality, the spore has in most cases approximately the same breadth whether it is measured from the inner side to the outer side, or seen in profile (i.e. tangentially - if the 4 spores are thought as four points in a circle). This means that the smaller diameter is almost identical in all positions the spore may take when it turns around its axis as often happens when the spore moves in the medium of a temporary preparation. There are, however, exceptions to this rule. The genus *Deconica* (now a group of species within the genus *Psilocybe*) is especially notorious for its spores being narrower in profile, and broader (about 1-2  $\mu\text{m}$ ) when turned around on their axis by about 90° (i.e. to a point where the position of the hilum coincides with a continuation of the geometrical axis and the spore is seemingly symmetric; Pl. 13). Such spores are called lentiform in spite of the fact that they are not subcircular in circumference but rather oval. Lentiform spores also occur in *Conocybe* and in *Coprinus*, but here, too, the character has no more than specific value though Fayod proposed a separate genus for those *Coprini* that show it. It is remarkable that many lentiform spores are slightly to distinctly rhomboid to rounded-(hex-)angular and elongated, i.e. they have an inaequilaterally hexagonal outline (shape of benzene ring formula) in frontal view.

The inner side is either convex or flattened or depressed, especially in the region just above the hilum, or in the lower half. We therefore speak of spores as having (or lacking) a suprahilar appplanation, or a suprahilar depression.

The elongate spores are called ellipsoid (Pl. 68 A, 1-6, 69, 2 sp) or ovoid if their Q (length divided by breadth) is smaller than 2; otherwise, they are called ellipsoid-oblong (Pl. 76, 11), fusoid (Pl. 75, 3-4) or cylindric (Pl. 72, 8), more rarely (especially in *Marasmius* and *Tylopilus*, sometimes *Boletus*) clavate with the club-end above (Pl. 60, 1 sp.). Cylindric (rarely fusoid or ellipsoid-oblong), white or pale-colored spores are characteristic for wood-inhabiting species (yet, of course, by far not all xylophilous species have cylindric spores), and even more for Polyporaceae where this shape is a family character.

Among the species with angular spores, Romagnesi distinguished two types, an axially symmetric and an asymmetric type. Usually a good indication of symmetry (Pl. 12, 1; 16) is the presence of a right (90°) angle at the lower end of the spores when the spores are seen frontally (i.e. with the hilum in line with the geometric axis), whereas in asymmetric spores, the lower end forms a larger angle\*. Since these two main types are known to exist - along with a series of subtypes - only in a single genus, *Entoloma*, we refrain from a more detailed discussion of this problem (but see p. 709).

In two genera the spores are visibly angular only in "upright" position, i.e. if seen from one end, with the longer axis of the spore vertically pointing at the objective. The sides between the angles are, in this view, either plane or slightly concave, and the number of angles varies from 5 to 10 (it is most frequently either 6, 8, or 10).

\*For a more thorough understanding of Romagnesi's spore types, it is necessary to study his paper, *Bull. Soc. Myc. Fr.* 53: 319-338. 1937 in connection with Pegler & Young, *World Pollen and Spore Flora* 7, 1978. The latter distinguish twelve spore types. Since these are important only in one genus, *Entoloma*, we do not describe them here; their taxonomic significance in *Entoloma* will eventually become obvious.

When seen in profile or in frontal view with the long axis being horizontal, these spores hardly show much unevenness and will easily pass as smooth (*Clitopilus*, Pl. 10, 75, 9) or warty-rough (*Rhodocybe*) unless the angles are slightly projecting into subalate striae. This character is of an undeniable importance in the taxonomy of the Entolomataceae, and has also been observed in spores with "removed" \* ornamentation of *Melanoleuca* (Tricholomataceae).

### *Ornamentation and wall structure*

The walls of the spores are either smooth and homogeneous or ornamented \*\*. Locquin (1942) distinguishes 3 types of ornamentation, viz.

1. *The primitive ornamentation (ornementation primitive)*. It disappears soon because of the growth and the further differentiation of the wall, and leaves usually no traces on the mature spore. Locquin who is inclined to think that it may be interpreted as phylogenetic reminiscence, suspects that certain ornamentations of primitive species might be traced back from derived species with primitive ornamentation. If so - and the thoughts of Locquin are theoretically not incorrect -, the primitive ornamentation in this case does not become identical with the secondary ornamentation which is the persistent and final one. If only one persistent ornamentation exists, there seems to be little to gain by calling it any more technical names than simply - ornamentation. The primitive ornamentation has been observed but not rediscovered, in *Macrolepiota procera* where the mature spores are completely smooth; it does not exist in the majority of the species of *Agaricales* but exists in some *Thaxterogaster*

2. *The secondary definitive ornamentation (ornementation secondaire, définitive)*. This said to be the final persistent ornamentation originating in the episporium, the exosporium, or in any of the layers of the spore wall proper (not in the perisporium). However, Josserand, two years earlier, has distinguished the fundamental ornamentation in the Russulaceae, which excludes the exosporial ornamentation which is of later origin and should be known as secondary ornamentation if this latter term were applied at all (the author prefers the term "exosporial ornamentation").

3. *The perisporial ornamentation (ornementation perisporique, evanescente)*. This is of perisporial origin (for the term perisprium, see below, p. 77), and is fugacious, becoming ruptured into patches and warts much in the manner the volva of an *Amanita* is ruptured and finally obliterated by dissolution or lack of elasticity.

\* This means with the amyloid exosporium dissolved according to the method employed by Josserand (1941).

\*\* Measurements of the spores are here (as in other papers by this author) always taken including the ornamentation but without the hilar appendage; this is the logical procedure which has also been recommended by R. Maire (1907, 1910) and adopted by the majority of authors. The spores minus the ornamentation would be the sporoid (Locquin), i.e. the volume of the spore without its ornamentation or superficial adhering material. Those authors who, for some reason, choose to give the measurements of the sporoid rather than that of the complete spore, should indicate this in order to make their measurements comparable, with those of other authors. Care should be taken to avoid measuring the hilar appendage as if it were part of the ornamentation!

This classification of the ornamentations cannot at present be applied in all cases because it requires very exact studies of the fine structure of the walls and their metachromatic properties against a series of dyes and reagents, as well as a study of the development of the spore from its first appearance at the tip of the sterigma till maturity. Consequently, in many cases, it is wise to speak of ornamentation in the general sense of the word. In contrast to the anatomical-ontogenetic classification it is always possible to apply the classification of typical configurations of the spore ornamentation in the Agaricales\*; these configurations are marked with Roman numbers.

*Type I.* Coarse banded ridges form a reticulated surface (*Strobilomyces floccopus*, *Boletellus retisporus*, *Lactarius lilacinus*). (Pl. 13, 1; 73, 2; 87)

*Type II.* Ridges and fine lines and warts form a reticulated surface (*Russula mariae*). (Pl. 87)

*Type III.* Warts or spines connected to form a reticulation.

*Type IIIa*, which signifies a complete network as in *Russula emetica*. (Pl. 87)

*Type IIIb*, which signifies an incomplete network. (Pl. 87)

*Type IV.* Warts or spines connected by scattered thin lines, not forming a reticulation or a fragment of a reticulation. (pl. 73, 6; 87)

*Type V.* Warts or spines from which short, thin lines run over the surface of the spore wall but do not reach the nearest wart or spine. (Pl. 63 A, 1.)

*Type VI.* Warts or spines completely isolated (*Russula schiffneri*, *Laccaria echinospora*). (Pl. 63 A, 2, 4, 5; 87)

*Type VII.* Punctations and fine, short lines, sometimes touching or crossing each other (*Russula melliolens*) (Pl. 87)

*Type VIII.* Catenulate warts usually crowded into or connected to chain-like rows (*Russula mustelina*) (Pl. 87)

*Type IX.* Ornamentation continuous, a smooth surface resulting (young spores of Russulaceae, retarded spores of *Gymnopilus cacaophyllus*). (Pl. 11, 2.)

*Type X.* Longitudinal ridges, often slightly spiralling, often somewhat anastomosing: *B. ananas*, Pl. 73, 7).

*Type XI.* Short warts or cylinders perforating a heterogeneous wall or covered by a smooth persistent wall-layer (*Porphyrellus gracilis*, *Boletellus betula*, *Metraria*, *Chromocyphella*, *Crepidotus*, sect. *Echinosporae*, *Melanomphalina*) (Pl. 13, 2-3; 73, 5).

In this work, type XI is used for spore ornamentations of the kind defined above as seen in light microscopy whether or not EM images bear out what light microscopy shows. SEM photos cannot show this particular structure of the spore wall. In EM sections, this type may reveal itself as a variant of type VI, VII or the *Continarius*-type (see chapter XVIII).

\*In other fungus spores, more types have been distinguished (short-ridged, loculate, etc.).

Type XII. Surface irregularly warty-roughened (*Tubaria dispersa*) cf. Cléménçon 1977.

In descriptions, the use of the figures designating the type of ornamentations, or a number of these figures combined (the unusual ornamentation in a species given in parentheses) shortens the descriptions considerably while still maintaining a high degree of precision, and is generally recommended, especially for those groups that, like *Russula* and *Lactarius*, have a great variability in spore ornamentation according to species, subspecies, varieties, individuals and individual spores. This scheme of ornamentation types is not concerned with the fundamental nature of the ornamentations, i.e. with the questions by which layer and by which process in the development the ornamentation of the spore is formed; isolated warts in a spore layer beneath the perisporial ornamentation in some Galerinas, isolated spines in *Russula schiffneri*, and innate (fundamental) spines in *Laccaria echinospora*, all correspond to the definition of type VI, yet the chemical character, the development, and the homologies of these ornamentations are by no means identical\*.

The following discussion of the structure of the spore walls in Agaricales is based on observations with the light microscope exclusively. It sums up all the observations made before a systematical study of electronmicroscopical spore sections has modified or clarified some of these observations. An attempt of coordinating these observations with the recent ones based on observation with the scanning microscope (Pegler & Young 1971, 1972) and on EM sections (Cléménçon 1968-1972) has been made in chapter XVIII which should be consulted in this connection.

The spore wall is in many cases simple or seemingly simple (Pl. 52 sp; 54 sp; 55 sp; 57 sp; 58, 3; 59 sp; 60 sp; 61 sp; 62 sp; 63 A 3) i.e. under the prevailing method of investigation, it cannot be recognized as double or complex. In the Agaricaceae, and in the related dark-spored families, the spore walls often consist of two or three layers, easily distinguishable in ammonia, KOH, or Melzer's reagent, and in cresyl blue solutions. These layers have a varying relative diameter. The inner layer is called the endosporium\* (De Bary 1881) (Pl. 12; 16; 21; 63 B 2, 5; 67, 2); the external layer is called the episporium (De Bary, 1884) (Pl. 12; 16; 21; 63 B 2, 5; 67, 2). Sometimes there is an intermembranal layer or what appears to be an intermembranal space (*Chlorophyllum molybdites*), and in some species (*Macrolepiota procera*), the endosporium has two layers, the internal and the external endosporium (Locquin 1942). In other instances, there is a third, often ruptured or saccate structure present that envelops the whole spore like a bag, or fragments of a hyaline covering. This part of the spore is called the perispore (Pl. 11, 2; 67, 5). It is very evident in such forms as *Galerina* sect. *Calyptatae* or *Strobilomyces floccopus* (Pl. 73, 1), in the

\*More data on the spore development and the micro-structure of the spore walls and ornamentations can be found in Locquin's papers on this subject (see literature).

\*\*It is important to distinguish between two similar terms: endosporium - the innermost wall of the spores, and endospore - a spore formed endogenously, inside an ascus or sporangium. Some authors carelessly refer to the endospore when in reality they mean the endosporium of a basidiospore. The Latin equivalents are endosporium and endospora respectively.

latter case strongly reminiscent of what is known in *Scleroderma cepa* and other species of that gastromycetaceous genus. Even in *Russula* (e.gr. *Russula archaea*) such enveloping layers have been noticed. Lohwag (1937) stated that they (or the outer part of them) continue the outer part of the basidial-sterigmatic-wall which is usually either so closely agglutinated, or so fugacious that no trace of it can be seen in mature spores.

In the literature, there is also indicated another term, exosporium. The exosporium was first given by the pre-Fayodian authors, e.gr. De Bary, as a synonym of episporium. However, the word episporium was preferred. Fayod himself, unfortunately mixed up the terminology as has later been shown by R. Heim (1931)\*. What Fayod called exosporium is a layer outside the episporium. In some cases, Fayod may have taken the optical halo as an outer layer, as was suspected by Heim but Locquin has proved that a true exosporium in the sense of Fayod actually exists in many cases, and that this exosporium had thus far escaped the attention of all authors except Fayod. There can be no valid reason to prefer Fayod's terminology to the use of the term episporium in the sense of De Bary and the French authors (starting with Patouillard), and the term exosporium in the sense of Locquin.

Consequently, in the most complex spores known, we have to distinguish between the following layers of the wall and its outer envelope (from inside outward):

1. The internal endosporium.
2. The external endosporium: both colorless, usually thinner than the episporium, or equally thick, sometimes seemingly or really absent (in monostratous spore walls).
3. The episporium: in the colored spores, this is the pigmented portion of the spore wall; in hyaline spores, it is always the thickest layer of all, and frequently shows an ultrafiltering capacity for cresyl blue in watery solution. It is doubtful but possible that the episporium may also be composed of two layers in a few species (see Heim 1931, and Locquin 1943).
4. The exosporium: this is often colorless and consistently thinner or less continuous than the episporium, usually delayed in its dissociation from or deposition on the primordial episporium, often of different chemical structure as compared with the neighboring strata (perispore and episporium).
5. The perispore: a loosely attached pigmented layer that envelopes the spore as a bag, or a closely attached but fugacious layer that is usually destroyed by

\*What Fayod calls endosporium is not the endosporium of De Bary and of the modern anatomists but the episporium of De Bary and the French mycologists, a term adopted in this book. The true endosporium is called "la couche membraneuse du protoplasma" (Primordialschlauch of the German authors) by Fayod. It is perhaps not superfluous to mention here that it is incorrect to write epi-, exo-, meso-, or perispore, inasmuch as we are not dealing with spore types - as we do in the case of "endospore" - but with constituent parts of spores, and confusion is invited by permitting the same ending in both instances. Therefore, in spite of Josserand's protestations, it seems to us that the French authors who use the feminine gender for spore types, the masculine for spore parts (le périspore - das Perisporium-) - the perispore), are indeed the more discriminating terminologists.

dissolution or fragmentation in an early stage of the spore development. It is doubtful but possible that there are occasionally two sub-strata composing the perisprium (see Locquin 1943). Some authors also admit the existence of a mesosprium between epi- and endosporium.

Here again we understand the structures of the spore wall as given above with reference to light microscopy. What is revealed by electron microscopy is both more and less instructive. It is more instructive because it gives us a clearer, more detailed picture of the different layers, their extension and electron-density, but fails to give us the colors of the pigments, their chemistry and microchemical reactions, nor does it provide data on the action of reagents such as Melzer's or dyes such as cotton blue or cresyl blue, Congo red or carmine. Since the images obtained by light microscopy and those obtained by electron microscopy do not necessarily coincide, we agree with Cléménçon (see chapter XVIII) that spore wall structure under EM requires a special terminology.

These anatomical facts and discussions of terminology are not of a remote significance for the taxonomist but of primary importance. The spore, with all its characters, has become, more and more, one of the most important organs on which the taxonomy of the Agaricales is based. The descriptive data become simpler and more definite when they are based on exact anatomical observations, and the homologies become more evident. Comparison between the spores of different species must be based on the comparison of homologous parts of the spore. The consecutive observations of Malençon (1929, 1931), Josserand (1941) and Locquin (1943) have shown that the Russulaceae have a fundamental ornamentation formed by the episporium which is slightly colorable with Melzer's reagent; the zone above the hilum and the larger portion of the surfaces of the fundamental ornamentation are covered with a thin exosporial ornamentation which is disrupted and clings to the episporium by a certain adhesiveness of its own and an increased readiness for humectation of at least parts of the episporial surface, and it responds chemically to most tests for amidon. It can be dissolved by several chemical substances, such as concentrated  $\text{HNO}_3$ , and less uniformly by  $\text{NaOH}$ ,  $\text{KOH}$ , etc. in a heated concentrated solution. Thus, Josserand first bared the fundamental ornamentation of the *Russulae* and *Lactarii*; but in *Leucopaxillus subzonalis* after dissolution of the amyloseous or amyloid layer, he did not find any fundamental ornamentation; neither did the author on the related *L. cerealis*, using concentrated nitric acid. This means that the entire ornamentation of *Leucopaxillus* (at least those two species) is superficial, heterogenous, and exosporial. Josserand indicated for *Melanoleuca* that the fundamental ornamentation is likewise either absent or insignificant. This marks a difference between the Russulaceae and the *Melanoleuca-Leucopaxillus* complex which is most important considering the elongated spores of such species as *Russula heterospora* and *R. ventricosipes*, and their similarity with those of *Melanoleuca*.

It may be noted here that the ornamentation of the Russulaceae has been thought to be, in its entirety, of destructive origin, i.e. a layer, at first continuous, that because of the growth of the episporium breaks into more or less regular fragments. Josserand exempted the fundamental (now tectum) ornamentation from this rule

but thought it still applicable for the exosporial ornamentation (interstratum, see p. 86). However, Locquin offers a new hypothesis on the development that is a physical one: As the exosporium solidifies at a certain point in the maturation of the spore, it cannot cling to certain areas because of the physical differences which, according to Locquin are determined by the different organization of the micelles of the surface of the episporium. Whatever the fate of this explanation may be, it must be admitted that it is the only one that is in full agreement with all the facts available. It does not by any means invalidate Malençon's now classical series of spore configurations in the "Asteroспорées" i.e. the bridge between some Gastromycetes and some Agaricales probably leading from the *Hydnangium-carneum* group to the Russulaceae.

The warty spores of the Cortinariaceae (Pl. 15, 51, 53C, 81-3) have been studied equally carefully in recent years. One might assume that here the development of the ornamentation is, in the great lines, similar to that of the Russulaceae. However, EM-sections do not support this analogy and it would be a wise course to refrain from taking the obvious homologies for granted. The spore ornamentation of *Galerina* (Cortinariaceae) has in common with *Russula* and *Melanoleuca* a character that is important in any discussion of the ornamentation in these genera, and is also significant in taxonomy. I am referring to the round smooth (or comparatively smoother) area just above the hilar appendage on the inner side of the spores which we may name suprahilar area. If this area is partly amyloid (amylaceous) the amyloid area is termed suprahilar spot (tâche, Heim 1938) in the Russulaceae; if it is not amyloid and merely stands out by its smoothness and its delimiting (beach-like) line (well visible in NH<sub>4</sub>OH-preparations imbedded in Shear's mounting fluid or with the ammonia replaced by a 50 p.c. watery solution of chloral hydrate and, in amyloid spores, in the Melzer reagent, it has been called plage (Pl. 15, 81, 82, 83, 1) by Kühner (1926), and this term has been adopted without change in other languages than the French. If there is no delimiting line and the warts or punctations or ridges of the ornamentation are merely more scattered or smaller or even inconsistently present on the suprahilar zone, we cannot rightly speak of a plage, nor are the small smooth spots (not necessarily suprahilar!) on the spores of some Crepidotaceae real plage areas. The plage is one of the most important characters distinguishing the typical *Galerinae* among the Cortinariaceae, and the suprahilar area is one of the characters separating *Melanoleuca* from *Leucopaxillus*.

The wall and its layers are continuous in many species, in others, especially those with complex walls, the spore wall is partly or entirely interrupted or modified at the apex. This apical interruption or modification is either (1) a germ pore (Pl. 12, 2; 68, 2, 5; 72, 2, 3) i.e. an interruption or modification of some or all layers of the wall with the endosporium either intact or also modified to interrupted (examples: *Macrolepiota*, *Kuehneromyces*, *Bolbitius*, etc.) whereby the apex of the spores often appears as a hyaline or paler colored dot and the outline of the curvature of the apical zone of the spore becomes marked by a narrowly flattened or indented tip which if broad enough appears truncated; or (2) a callus, i.e. a thinner-walled apical region that is more or less convex, or even callously protracted rather than truncate (example: *Galerina* spp. Pl. 14). The callus has been named by Heim (1931) who

first distinguished it from the germ pore with which it was often confused before Fayod (1889). The germ pore has been known for a long time but its taxonomic importance has been stressed only by Fayod and Patouillard.

The germ pore of light colored spores is not always easy to recognize under dry objectives, and sometimes even under immersion lenses. It should be studied after an initial treatment with 10 p.c. KOH which is subsequently removed, and replaced by cresyl blue solution (see p. 89) or aceto-carmine and with phloxine.

Undoubtedly, the transition from a callus to a pore is not a quite sharp and mutually exclusive one. In *Galerina*, the callus is often pore-like insofar as a very narrow apical zone with modified wall structure and without truncation can be found in species closely allied to species with a typical callus. On the other hand, as soon as this apical zone becomes wider and more obtuse or truncate, a typical pore is at hand. In small spores with small apical wall modifications it is often impossible, even by the use of specific colorants and dyes and with the best light-optical means at the disposal of the observer using standard equipment, to make out what the modifications of the wall actually are and which layers of the spore are involved. A comparison of the illustrations given by the various authors will corroborate this point. In view of the importance of the character, it is worth while to study all typical and borderline cases with the help of spore sectioning and an electronic microscope\*.

These observations do not mean that the taxonomic use now made of pore and callus in agaric taxonomy is illegitimate unless more precise data are available. Wherever a certain definable structure can now be observed to characterize a taxonomic group, it should by all means be employed to the utmost. It is here merely suggested that a future investigation into the fine structure of the apical spore wall will help to put the descriptive data into more precise terms and help in the possibly useful establishment of different types of pores - hopefully of taxonomic value.

The microscopical basis of the macroscopical difference in spore print color is usually the pigmentation of the spore wall; most of the dark-spored families can be recognized from the spore color under the microscope; however, the cream-colored, green and pink shades in light-spored agarics and boletes are not always clearly reflected in the color seen under the microscope. Sometimes, the pigmentation of the spores under the microscope is of independent value in the taxonomy of certain groups (*Xanthoconium stramineum*; *Callistosporium*; *Callistodermatium*; *Pachylepyrium*).

### Size

The size of the basidiospores ranges from 2 to 48.5  $\mu\text{m}$  in length and accordingly in volume. All spores are unicellular, except for a few isolated cases where the old

\*Much has already been accomplished by the work of Meléndez-Howell (1967), Kühner and Besson & Kühner (1972) and Besson (1970), see chapter XVIII.

spores have been seen to become septate e.gr. in *Crinipellis mirabilis*, etc. (Pl. 60, 1; 63, 3d, e), after discharge. Heim (1948) interprets this as a direct transformation of the spore into a binucleate chlamydospore.

### *Attachment*

The spores are never sessile on the basidia in the Agaricales, in spite of Fayod's indication of sessile spores in his genus *Astylospora* which seems to be based on faulty observation. They are always borne on the apex of sterigmata that are apical and half-sickel-shaped or horn-shaped (e.gr. Pl. 75, 78, 80) in the Agaricales (very rarely lateral, a feature that has no taxonomic significance since it is an individual irregularity in an occasional basidium), or else provided with an apical spiculum which is curved outwards (*Hiatulopsis*-type, pl. 84, see also p. 111).

Near the base (and in the case of the Agaricales practically always distinctly in an eccentric position slightly off the geometrical longitudinal axis of the spore) is the hilar appendage\*, the minute wart- or cone-like tubulose excrescence which connects the spore proper (sporoid) with the tip of the sterigma. It is of variable size. In certain genera, it is particularly voluminous (so in *Mycenella*) and becomes thus an additional character of the spore, useful for taxonomic purposes.

### *Content*

The protoplasmic interior ("nucleus" of Corda 1842) is usually colorless; it often includes one to several oil-droplets ("nuclei" of some authors) which in size, number and arrangement are often inconstant and appear or disappear on drying so that they are of much less taxonomic value than they are in Discomycetes. Rarely does it contain hyaline or colored solid (leuco-) pigment bodies, especially in dehydrated spores of the genus *Callistosporium*, rarely in other Tricholomataceae and in the Bolbitiaceae.

\*We do not share Josserand's preoccupation with the word hilum. The "scar" on the detached spore exists and is rightly called hilum. It is found at the tip of the hilar appendage in most Gastromycetes. In the Agaricales, the region just above this hilar appendage (on the side where it protrudes eccentrically, i.e. the inner side) is logically the suprahilar region, and where there is a smooth spot, "plage" etc., this smooth spot or "plage" is the suprahilar spot or plage. Heim (1955), in part for other reasons, also favors the usual term, hilar appendage, and at the same time adds a number of additional terms (see there). Smith favors the term sterigmatal appendage; Josserand - apiculus (apicule), so as to avoid the word hilar. Pegler & Young (1969, 1972) adhere to Heim's (and my) definition.

*I. Surface markings*

The hilum itself has not been studied until recently (Pegler & Young 1969), obviously because of difficulties arising from direct observations with the light microscope. Pegler & Young, studying the hilar appendage ultrastructure by the preparation of single-stage carbon replicas (method of T.W.K. Young, *Proc. Linn. Soc. London* 179: 1-10. 1968) and examination with an electron microscope distinguish two main types of hilum structure:

(1) Nodulose type: Hilum asymmetrically borne on the hilar appendage pointing toward the inner (adaxial) side of the spore, consisting of an approximately circular area characterized by a number of small rounded protuberances, - no pore. This type is common in hyaline-spored Aphyllophorales (*Schizophyllum*, *Cantharellus*) and Agaricales (Polyporaceae, Hygrophoraceae, most Tricholomataceae, Amanitaceae, Entolomataceae, Russulaceae and Bondarzewiaceae), Pl. 47, 5, 8; 48,

(2) Open-pore type: Hilum similarly borne, appearing as a depression, not noticeably nodulose, often constituting a break in the wall continuity of the hilar appendage; on the other (abaxial) side of the hilar appendage there is a conspicuous pore or tear in the wall; the two sides are frequently joined by a circum-apical slit which may widen to produce a single elongated tear. This type is common in the Agaricaeae and perhaps exclusive in the Coprinaceae, Bolbitiaceae, Cortinariaceae, Crepidotaceae, Paxillaceae, Gomphidiaceae, Boletaceae, Pluteaceae. It is exceptionally found in the Tricholomataceae (Lyophylleae, Termitomyceteae), Pl. 45,

This new approach to the study of spore surfaces under the scanning microscope is undoubtedly valuable for the taxonomy of the Agaricales. Pegler & Young extended their studies, using the same method, to investigate and photograph spore surfaces in many genera of Agaricales (Pegler & Young 1971).

As had to be expected, the surfaces of light-microscope-smooth spores appeared often, not always, smooth under the scanning microscope. Where they appeared ornamented in scanning microscope view, the effect may have had its origin in (a) the limited dissolution power of the light microscope, (b) in the structure of the outer spore wall layer (which is often grossly fibrous in a seemingly unstructured matrix), (c) in folding, wrinkling or other artefacts due to the method applied.

Without parallel studies of ultra-fine sections of the spore wall, it is at present not always easy to see whether one or the other reason for unevenness has to be assumed. However, a few cases of surface markings are undoubtedly true ornamentalations such as the longitudinal ridges and sulci in spores of *Armillariella mellea* (Pl. 47, 3) and the small warts of the spores of *Kuehneromyces mutabilis* also observed by Clémenton (1972) in spore sections, yet the latter appear to be of a different category as compared with the very minute roughness of the wall surface in some Strophariaceae. In fact, the ornamentation of the genus *Kuehneromyces* should

actually be projecting enough and the wartlets spaced enough to be visible in the light microscope. This is not the case and we (see Cléménçon l.c.) believe that the reason can be found in the fact that, between the warts, a EM-dark mass, probably a gelatinous or mucilaginous substance, easily removable during the preparation, remains visible in the liquid media used in light microscopy and causes the spore surface to appear smooth. Similarly, many ornamented spores, even some that appear smooth under the scanning microscope and punctate in optical sections under the light microscope, have a smooth perisporial tegument above the ornamentation. this may well be the case in *Phaeolepiota* where the scanning microscope (Pegler & Young 1971) shows a smooth surface but a finely rugulose suprahilar region, i.e. the perisporial layer does not cover the suprahilar region producing the effect of a poorly differentiated plage in reverse. Some spores which under the best optical conditions in the light microscope view seem to have an ornamentation of type XI (immersed spinules), do not show an outer smooth layer in EM photographs (like those of *Crepidous sphaerosporus*) and the spinules forming the ornamentation appear free. Pegler & Young's plate 19, Fig. 1 and 2 suggest that there is indeed an outer perisporial covering which swells up in alkalic solution but adheres to the truncate cones of the ornamentation and collapses over them or disappears in the preparation of the spores for EM view. However, according to Cléménçon (1977) the EM and SEM picture is the correct one and the light microscope image is due to an optical illusion.

Undoubtedly, the already existing data provided by Pegler & Young\* are of importance for the taxonomist but as far as spore ornamentation is concerned we must hope for clarification of some remaining doubts about the nature and origin of the ornamentations as contrasted to the appearance of the ornamentations under the scanning microscope, and it must be hoped that further work including the study of more spores of more species will throw additional light on spore structure and its usefulness as an additional approach to taxonomy. Studies of this type, including sections of the spores will also contribute to a better understanding of the nature and variations of germ pore and callus ultrastructure.

## 2. Electron microscopy and spore teguments

by H. Cléménçon

Submicroscopic surface sculptures were made visible with either carbon replicas or by direct observation using the scanning electron microscope (SEM). The taxonomical and cytological value of this new information is considerably increased by the analysis of the wall layers in ultra thin sections using the transmission electron microscope (TEM). Both methods, SEM and TEM, supplement each other and in many cases their combined application is necessary for a satisfactory interpretation of the spore wall structure and of its taxonomical significance. Detailed research by many workers using the TEM (e.g. Perreau-Bertrand 1967, Meléndez-

\*I am grateful for permission to reproduce (plates 45-52) some of Pegler & Young's spore photographs which were originally published by these authors (1971).

Howell 1967, Besson 1969, Cléménçon 1970-1977, Besson & Kühner 1972, Capellano & Kühner 1975, Hugueney 1972) has lead to a wealth of new knowledge, and many new terms have been proposed to describe the observed structures of the spore wall teguments.

Whereas the traditional terminology based on light microscopy alone uses the relative position of the wall layers as the only criterium, the new terminology uses fine structure, chemical behaviour and partially also ontogeny of the layers, as observed in both, the light and the electron microscope. It soon became evident that the terminology based on the layers as they appear in the light microscope is not necessarily applicable to the electron optical findings. For this reason some authors (e.g. Cléménçon 1970) prefer to avoid the classical terminology altogether, whereas others (e.g. Kühner 1980) use a hybrid terminology that preserves old terms wherever this seems possible.

### *The basic model of the spore wall.*

Basically the spore wall consists of two classes of layers of teguments. The inner class is chemically and mechanically more resistant than the outer layer, which is gelatinous to mucilaginous and readily soluble in 5% potassium hydroxide or 5% chromic acid. Because of this higher stability the inner structures have been termed eusporium by Besson & Kühner (1972), and the outer, more mucilaginous structures are named myxosporium by the same authors. The analogy or probably homology with the inner and outer layers of the wall of the vegetative hyphae is striking and seducing.

The EUSPORIUM may be layered, and the layers may be grouped in two distinct teguments in the most highly differentiated spore walls. The layers are produced by different degrees of dispersion of an electron opaque substance in a transparent matrix (as seen after fixation with permanganate). Usually the opaque substance gets more and more abundant towards the periphery of the eusporium, often being (almost) totally absent in the innermost region, and sometimes being the only one present in the outermost region. The innermost, transparent region is called corium by Cléménçon (1970) and endosporium by Kühner (1980). If the outermost layer is totally opaque, it is called tunica by Cléménçon.

The model proposed by Cléménçon (1970) admits a more or less granular dispersion of the opaque tunica-substance in the transparent matrix of the corium-substance. Between the pure corium and the pure tunica, one or more layers of granular appearance may be present. Quite frequently these layers dominate the spore wall architecture by their great thickness, and often they represent the bulk of the spore wall. The tegument formed by them has been called sclerosporium by Besson (1970), coriotunica by Cléménçon (1970) and episporium by Kühner (1980).

Capellano & Kühner (1975) admit a very dense episporium in *Rhodophyllus (Entoloma)*, but distinguish a very thin, totally opaque and easily detachable layer (as seen in ultra-thin sections), the leptotunica, at the surface of the spores.

The MYXOSPORIUM may be a simple and thin mucilaginous layer covering the spore. It then probably represents the residual gelatinized basidial wall of the apophysis at the tip of the sterigma. Therefore it is called sporothecium by Cléménçon (1970), but Kühner (1980) prefers to call it ectosporium.

In many cases a much more elaborate and differentiated region is present between the superficial sporothecium and the euphorium. This region, called perispore by Kühner, forms most of the known surface ornamentations of the spores (at the present time we cannot generalize because of insufficient number of observations), but it may also be completely smooth.

Ultrathin sections reveal an amazing variety of different fine structures and architectures of the spore ornaments in the different genera and families of agarics, but a main sequence of developmental steps seems to be widespread. First, by an unknown mechanism an electron opaque layer, the primary mocostratum, is formed between euphorium and sporothecium. This layer seems to be gelatinous, soluble in potassium hydroxide and can often be visualized in the light microscope by staining it with cotton blue. With maturation of the spore the primary mocostratum frequently solidifies locally to form harder, more resistant and more electron transparent grains that sometimes form a continuous or interrupted network or layer on the spore. The substance left between these grains is frequently liquefied so that a rough, warty or otherwise ornamented surface results.

In the Cortinariaceae the transformation is gradual, resulting in a type of myxosporium called epitunica by Cléménçon (1970, 1973), but in the Russulaceae the change is more abrupt and very localized, resulting in the hard tectum and the mucilaginous interstratum covering it.

#### *Modified types of spore walls*

It is interesting to note that in many genera the spore wall is much simpler than the model described above. Most Tricholomataceae have a spore wall very comparable to the wall of the vegetative hyphae. This may be interpreted as a secondarily reduced state, where the sporothecium replaces the lost spore wall. Viewed this way, the simple, thin walled, colorless spores of these fungi would be an end state of a long process of exogenisation leading from a fully walled endospore to a real exospore (Cléménçon 1977a). On the other hand the simple spore wall may be considered primitive. Basidiospore formation in these fungi may be analogous or even homologous to the budding of yeasts, the bud representing a primitive spore that is not yet capable of forming a proper spore wall. We have little to help us to decide which hypothesis comes closer to reality.

Within the Cortinariaceae all stages of a reduction of the epitunica so characteristic for this family can be observed in different species. Many species of *Cortinarius* bear a well developed, highly structured and colored myxosporium (Cléménçon 1973), but the spores of the closely related *Leucocortinarius* lack the epitunica and are smooth and hyaline. A less pronounced reduction of the epitunica can be seen in many very faintly ornamented spores of *Galerina* or *Hebeloma*.

Some elaborate spore wall architectures are typical for some families or genera of Agarics. The Entolomataceae (plate 53 fig. A) are characterized by the presence of an opaque and (almost) structureless tunica lying over a well formed, transparent corium. There is no intergrading of the two layers, but the ribs of the spores of *Rhodophyllus* are stuffed with a spongy mass called epicorium.

In contrast to this, most colored spore walls of the Agaricaceae, Coprinaceae, Bolbitiaceae, Strophariaceae, Cortinariaceae and Boletaceae present a well developed, thick and frequently also layered coriotunica (sclérosporium, episporium). The smooth spored genera of these families usually lack a well developed myxosporium, whereas the ornamented spores bear a thick and internally characteristically structured myxosporium called epitunica (plate 53, fig. C).

The eusporium of the Russulaceae (plate 54) is simple, but the myxosporium is very well differentiated. During maturation the primary mucostratum located between the sporothecium and the eusporium condenses into the hard, compact, electron transparent tectum leaving some opaque mucilaginous interstratum between tectum and sporothecium. The tectum forms the inamyloid warts of the spore wall, the interstratum the amyloid mass covering them.

The Tricholomataceae as defined in this book embrace species with thick walled coriotunica (e.g. *Oudemansiella mucida*, plate 53, fig. B), species with spiny spores of a unique fine structure (*Laccaria*, Besson 1971), species with ornamented spores reminding us very strongly of the *Russula*-spores (*Melanoleuca*), as well as species with thin walled, smooth spores whose walls are not significantly different from the hyphal walls (e.g. *Mycena*, *Marasmius*, *Tricholoma*). We are not ready at this time to attribute to this diversity some real phylogenetic meaning, although in many cases (*Laccaria*, *Melanoleuca*) its taxonomic importance seems obvious.

The Crepidotaceae are in a similar, although less complex situation. The smooth spored *Tubaria*-species have a wall consisting only of a reduced, thin and soft coriotunica (Clémenton 1977b), whereas the ornamented spores of *Crepidotus* have a fully developed eusporium bearing a special but unnamed type of myxosporium (Clémenton 1977c).

### Bibliography

- BESSON, M.A. (1969) - Structure de la paroi sporique des *Rhodocybe*, *Rhodotus* et *Clitopilus* (Agaricales). C.R. Acad. Sci., Paris. 269: 142-145.
- BESSON, M.A. (1970) - Ultrastructure de la paroi sporique amyloïde et ornée de quelques Hyméno-mycètes. C.R. Acad. Sci. Paris 271: 964-967.
- BESSON, M.A. & R. KÜHNER, (1972) - Recherches morphologiques et ontogéniques sur la paroi sporique et le pore germinatif des *Panaeolus* (Fr.) Quél. (Agaricales). C.R. Acad. Sci. Paris 274: 1915-1920.
- CAPELLANO, A. & R. KÜHNER (1975) - Architecture de la paroi sporique des Volvariaceae (Basidiomycètes - Agaricales) en microscopie photonique et électronique. Bull. Soc. Linn. Lyon 44: 4-21.

CLÉMENÇON, H. (1970) - Bau der Wände der Basidiosporen und ein Vorschlag zur Benennung ihrer Schichten. Z. Pilzk. 36: 113-133.

CLÉMENÇON, H. (1973) - Die Wandstrukturen der Basidiosporen III. Cortinarius und Dermocybe. Z. Pilzk. 39: 121-144.

CLÉMENÇON, H. (1977a) - Die Strukturen der Basidiosporenwand und des Apikulus und deren Beziehung zur Exogenisation der Spore. Persoonia 9: 363-380.

CLÉMENÇON, H. (1977b) - Die Wandstrukturen der Basidiosporen. VII. Tubaria. Z. Pilzk. 43: 283-289.

CLÉMENÇON, H. (1977c) - Die Wandstrukturen der Basidiosporen. VI. Crepidotus sphaerosporus und verwandte Arten. Z. Pilzk. 43: 269-282.

HUGUENEY, R. (1972) - Ontogénèse des infrastructures de la paroi sporique de *Coprinus cineratus* Quél. var. *nudisporus* Kühner (Agaricales). C.R. Acad. Sci. Paris 275: 1495-1498.

KÜHNER, R. (1980) - Les Hyménomycètes Agaricoïdes. Num. spéc. Bull. Soc. Linn. Lyon 49, Juin 1980.

MELÉNDEZ-HOWELL, L.M. (1967) - Recherches sur le pore germinatif des Basidiospores. Ann. Sci. Nat., Bot., Paris. Sér. 12, VIII: 487-638.

PERREAU-BERTRAND, J. (1967) - Recherches sur la différenciation et la structure de la paroi sporale chez les Homobasidiomycètes à spores ornées. Ann. Sci. Nat. Bot., Paris, Sér. 12, VIII: 639-746.

## XIX. STAINS, MACROCHEMICAL COLOR REACTIONS AND CHEMICAL ANALYSIS

Absorption of specific dyes is not a direct expression of the chemical constitution of the various parts of the plant tissue, yet in certain cases, the absorption of the dye is different in different organs and different in different parts of hyphal or sporal walls, etc. This so-called metachromasy is not the same in the same organs of all Agaricales, and Kühner, Singer, and Heim successfully used this fact as the basis of taxonomic as well as organographic differentiations, i.e. for the characterization of groups in the classification of the Agaricales and for the characterization of certain specific types of organs. These metachromatic colorations like the chemical reactions which also have been introduced into agaricology since 1907, are only characters, and are not pretended to be more than that. Some authors speculated on the chemical nature, and the physico-chemical conditions under which these selective colorations and color reactions take place; in some instances, the substances involved have been studied to a certain degree, from a chemical point of view, or else the type of reaction taking place was too obvious to be overlooked by the mycologists, yet, as a rule, no systematic attempt has been made to identify the reacting substances by a standard method of chemical analysis, and to explain the reactions taking place in a biochemically proper manner. The notable exceptions that might be mentioned here are the poisonous agents in a very small number of poisonous fungi, especially *Amanita* and the hallucinogenic ("psychotropic") substances recently discovered in *Psilocybe*.

This, in the opinion of most modern mycologists employing chemical characters, does not render them any less valuable from the taxonomic point of view. The only requirements of a good character are its constancy and correlation with other

characters. Those who have in the last 60 years systematically introduced new chemical characters had only two preoccupations: (1) are the reactions obtained genotypical - or phaenotypical and accidental, i.e. are they reactions typical for the form under consideration, or dependent of factors such as temperature, substratum, or host, and consequently irrelevant for taxonomic purposes; (2) are these reactions correlated with morphological characters?

Even if the chemical substances involved in the reaction are unknown, or the modus of their transformation hypothetical, their taxonomic value may thus still be considerable, and arguments in questions of systematics based on chemical characters may still be valid provided that the chemical character is both genotypical and correlated with morphological characters.

This does not mean that an investigation of such reactions from a purely chemical point of view might be omitted in the future. It is obvious that work of this order is highly desirable. An attempt has been made to correlate both taxonomic and chemical research in lichenology especially as far as the isolation and identification of lichen acids were concerned, and the results have been interesting and valuable both from the chemical as from the taxonomic point of view.

The only objection that may be made to the taxonomic use of "good" chemical reactions as characters in spite of the lack of a chemical explanation of the changes observed, is that an equal external effect may be obtained by using the same method with different species even though the substances involved may be different. The error in our interpretation would then be the application of a term such as "positive" or "amyloid" for a reaction of a certain order in all cases whether they are due to the presence of an identical substance or merely of a substance with identical or similar reaction in contact with a given reagent. It is, of course, probable, or almost certain, that the amyloidity of spore ornamentations or spore walls is not based on the presence of the same substances in all cases where a "positive" reaction with an iodine reagent is obtained. In fact, the apices of the ascii of certain Ascomycetes (pure blue reaction with Melzer's reagent), the ornamentation of the spores of the genera *Melanoleuca* and *Leucopaxillus* (blackish violet), the hyphae of *Marasmius* and *Mycena* (vinaceous to vinaceous brown), and the hairs of *Crinipellis*, *Chaetocalathus*, *Lachnella* (brownish violet to deep reddish brown), the spore walls of *Neohygrophorus angelesianus* (pale greyish livid) and the "amyloid" intercellular material in *Chroogomphus* (and *Brauniellula*) are probably of a different chemical composition, and the amyloid reaction is not caused by the same substances, or the same group of substances, but by a physical effect common to all materials of each of the groups quoted above as example.

All these observations may well be justified as stated. Yet, if an argument concerning a taxonomic question, and based on chemical characters, is only one part of a series of reasons that support, for example, the affinity of two taxonomical groups, the chemical character should not be disregarded on theoretical grounds. The overemphasis put on a chemical character alone (e.g. in Melzer & Zvára's monograph of the *Russulæ*) is not justifiable even if the chemical identity of the reactions in each case could be demonstrated by analytical means. This does not

make the discoveries of Melzer & Zvára any less valuable for the use by an experienced taxonomist. Those who reject chemical characters must also reject color, odor, taste, and gelatinosity which are likewise characters without a fully explored chemical basis in most cases. We would then have to rely on morphology alone - and morphology, at present, does not provide complete guidance either. It is therefore necessary to use, with the utmost caution, but without blind reluctance, all available characters, the more - the better. Biology is not yet a strictly exact science, and asking to consider it as such without allowing for a large number of working hypotheses, is equivalent to stopping its development.

Alan Burges (in Lousley, J.E., Species Studies in the British Flora, London, December 1955) says correctly: "From time to time, attempts have been made to apply chemical tests to the identification of fungi and lichens. This has often aroused most violent partisanship, and the sensible view that the chemical tests simply add one or two more characters to the already recognized morphological characters is surprisingly seldom taken. In a group which is already difficult and in which characters are few or very variable, one would imagine that any additional evidence would be welcome" (p. 78).

These observations are necessary in order to introduce the use of chemical characters to a broader public than has been possible before. The acceptance of chemical characters as a valuable contribution to the factual material available for the determination of affinity is not in danger since even the critics of this method make widest use of it in their own papers. However, unreasonable criticism is merely another factor in delaying the broader application of chemical characters among the mycologists, including collectors data and routine determinations.

### *Metachromatic stains*

Cresyl blue mounts of spores of *Macrolepiota*, *Leucoagaricus* and *Leucocoprinus* allow the observation of the endosporia because of a selective coloration that results from ultrafiltration of the dye solution by the episporium in such a manner that the endosporium is dyed reddish, and therefore stands out enough to be rather conspicuous even in cases where it is not very strongly developed. In other genera of the Agaricaceae, the endosporium - whether strongly developed or not - does not show such an effect in cresyl blue mounts. This differentiation has been shown to be of great help in the subdivision of this family, as an additional spore character to be used together with the iodine reaction and the germ pore. It has also been shown (Pouzar 1966) that the spores of certain species of *Gerronema* (*G. splendidissimum* and *G. venustissimum* - "*Haasiella*") have metachromatic spore walls in cresyl blue mounts. This has been corroborated by me but it does not seem to be a character of generic status. Spore and other elements are often also more or less metachromatic in certain species of other genera, particularly polyporaceous ones.

In the hyphae of the stipe, cresyl blue often provides a similar character based on metachromasy which is somewhat but not quite parallel with the Melzer reagent's

metachromasy (see p. 92-96). Kühner who has discovered both the sporal and the hyphal metachromasy in cresyl-blue mounts has first indicated several important differences between the positive reaction with the Melzer on one hand and the metachromasy with cresyl blue on the other hand (1933). This made the use of cresyl blue in addition to that of the Melzer even more important. The sections can be treated with ammonia or KOH at first in order to separate the hyphae, but the alkaline solution must be removed entirely afterwards; the section is then colored with a watery solution of cresyl blue, the excess dye is removed with filter paper, and replaced by water. In certain species such as most *Mycenae*, many *Marasmii*, etc., the hyphae of the stipe become red, thus contrasting with the normal coloration of hyphal walls obtained by cresyl blue which is a pale violet, pale blue, or practically nil. The cortical layer of the stipe should be disregarded for this purpose.

For the red metachromatic stains produced by cresyl blue in the spore walls and hyphae, this dye can also, often advantageously, be replaced by toluidin blue, with identical results.

A strong deep blue stain is obtained by the use of cresyl blue on the interior of all gloeocystidia, in some Corticiaceae, *Gloeothallus*, *Favolaschia*, etc., and in the agarics (Pl. 21, 3); this characteristic metachromasy is, as we have seen above, a perfect means for recognizing these bodies in dubious cases (Singer 1945, Heim 1946). The technique is the same as described above.

Kühner has also indicated (1934) "very numerous precipitations of a bright red color" in several Hygrophyses (especially the species with viscid stipe) which is not generally observed in other fungi; the walls of the cystidia are colored either metachromatically (deep lilac or violet, or the same color but very pale, Pl. 2, 2; 21, 5), or blue (*Inocybe*, Pl. 17; 18; 19); reddening (metachromatic) trama is found in most of *Agrocybe*, *Hygrophorus*, *Mycena*, *Lepiota*, and *Hebeloma* species studied by Kühner, never in *Cortinarius*, *Inocybe* or *Naematoloma*; strong reddening of the trama of the Amanitaceae is observed in the subgenus *Lepidella* (excepting the *Phalloides*-group), and in the *Emetica*-group of *Russula*, the basidia are distinctly metachromatic in many agarics (*Tricholoma*, *Cortinarius*, and others) but never in the Boletaceae.

Cresyl blue can also be used in order to study the ornamentation the same way as is done in the Russulaceae with Melzer's reagent; cresyl blue has given a picture surprisingly similar to an exosporial ornamentation of the type IIIb-IV-(V) in *Russula*, when used on spores of *Neopaxillus echinospermus*. The exosporial ornamentation of the Cortinariaceae is also deep violet colored but usually less well differentiated from the episporium, at least optically (this is also the case in *Thaxterogaster*).

Cresyl blue is not the only dye that provides the anatomist, working on Agaricales, with metachromatic colorations. Several more with diamine blue, alkaline methylene blue, various violets, carmines, etc.) metachromatic stains are known, but their use has not yet become taxonomic routine (see f. ex. R. Sandor, *Zeitschr. f. Pilzk.* 25: 108-111. 1959).

Cotton blue\* has become a very valuable help in the study of the ornamentation of the Discomycetes (Le Gal, Discomycètes du Maroc I. *Bull. Soc. Myc. Fr.* 76: 115-177. 1958) and has given important results in the study of the spore ornamentation in such agaric genera as *Crepidotus* section *Echinospori*, *Melanomphalia*, *Fayodia* and *Lepista* as well as in *Porpoloma* and *Metraria*. But as Kotlaba and Pouzar (1964) have shown first, and was later shown in a survey of nearly all genera of light-spored agarics and boletes as well as closely related or similar non-Agaricales (Singer 1972), the importance of this dye goes far beyond the recognition of the configuration of the ornamentation in certain species. It has relevance in the taxonomy of the Agaricales (as in the Aphyllophorales and Gasteromycetes) since in some species the dye is taken up by the spore wall or ornamentation while in others it is not. In certain genera, this character assumes generic value. In certain cases, it can also be applied for hyphal walls and the walls of the hymenial elements and the surface hairs (as in *Crinipellis*). Wherever a wall or parts of it take up cotton blue so as to show a contrast with the interior of the cell or with other parts of the wall, it is called cyanophilous, otherwise acyanophilous (Kotlaba & Pouzar 1964).

For these purposes, cotton blue solution is prepared by dissolving it in lactic acid:

Cotton blue	0.05 g
Lactic acid	30 g

The solution should be 20 hours standing while it is periodically shaken and then filtered. The action of the cotton blue is accelerated by boiling the preparation, and even after this it is recommended to make the final observation only after several minutes or hours.

Congo red\*\* has thus far given interesting results in the Aphyllophorales, but also in the Agaricaceae (see Kühner & Romagnesi 1953 and Weresub 1971 - see under *Chlorophyllum*, p. 111).

For the study of the metuloids of *Inocybe*, C. Bruylants (1955) recommends pyronin\*\*\*.

This brings up the question which dyes are recommended for general use in Agaricales. For routine preparations of an unknown agaric or bolete, it is customary to use ammonia-mounts\*\*\*\* first without any dye; it is not wise to start the study of a species with stained material. Only as a second step, in order to get

\*Cotton blue is not a dye of uniform chemical composition and therefore a definite make must be used for all studies of comparative anatomy. In our work we have always used cotton blue of Swiss manufacture (see Singer 1972).

\*\*Saturated solution of Congo red in concentrated NH<sub>4</sub>OH. On drop of this and one drop of 5% KOH are directly applied on the object.

\*\*\*\*"Put a (dried) fragment of the lamella at first in a drop of ammonia and keep there one minute, a (dried) fragment of the stipe three to five minutes, dry over blotting paper, then soak well in a drop of pyronic acid (1% waters solution)."

\*\*\*\*KOH is preferred in tough species or in species with dense tissue that are not mercerized easily by NH<sub>4</sub>OH, also in preparations that are intended to show the general structure of an organ, as in KOH strong pressure on the cover glass can be avoided. However, for a study of fine structure such as diverti-

clearer pictures, this same preparation may be dyed with phloxine (now frequently used by American specialists of Higher Basidiomycetes), 2 p.c. alcoholic solution, which is stable in ammonia or even KOH mounts. Phloxine is, however, taken up by the interior of the hyphae more than by the walls, and for the walls, cresyl blue is as good as any other dye for a first try. As a rule, every fungus and every organ, and even every part of this organ requires individual stains, according to their chemical constitution and physical properties. In many cases, chemical reagents will be used, such as Melzer's reagent, in preference to organic dyes.

### *Microchemical reactions*

It is difficult to differentiate between dyes and reagents since many reagents, among others the most important reagent for the study of Agaricales, Melzer's reagent, act rather by absorption than by fully measurable chemical transformations of the treated material. However, even though the Melzer reagent is, in a certain sense, an inorganic dye causing metachromasies of the same order as cresyl blue, it is currently considered a reagent rather than a dye. It was unavoidable to mention the Melzer reagent in the preceding chapters, but we shall now attempt to give a resumé of the reactions that can be obtained with it.

The reagent has completely replaced the use of any alcoholic iodine solution and the classical use of  $ZnCl_2 \cdot J_2$ . Its composition though slightly altered in one sense or another (without much difference in effect) by some mycologists is still the original one indicated by Melzer (1924).

KI	1.5 gr.
Iodine	0.5 gr
Water	20.0 gr
Chloral hydrate	22.0 gr.
<hr/>	
	44.0 gr.

It has first been used on the "exosporial ornamentation" i.e. the interstratum of *Russula* spores and this was its original purpose. However, the mycologists who later searched for all kinds of positive iodine reactions in the tissues and spores of the Agaricales, found in Melzer's solution a convenient standard solution that would always give identical results if applied in an exactly circumscribed manner. It cannot be emphasized too strongly that any deviation from the formula and the following procedure, may (not must) cause a discrepancy between the results obtained and those described by the authors.

The preparation must first be wetted for a few seconds in ammonia ( $NH_4OH$ -concentrated), then the ammonia must be completely removed with filter paper, and a large excess of Melzer's reagent must be added in order to compensate for any alkaline reaction still prevalent immediately around the fragment examined.

culation of epicuticular hyphae, pigment incrustations, and spore ornamentations, KOH is often inferior to  $NH_4OH$ . Spore color is often quite different in KOH and  $NH_4OH$  mounts. For observation of gelatinous layers KOH is preferred.

Usually, a positive result can be seen without prolonged action of the iodine, yet if the result seems to be negative or unequal or doubtful at first, it is recommended to re-examine after about 20 minutes waiting.

The reaction is called amyloid or pseudoamyloid - if positive - and inamyloid, if negative. The amyloid reaction is nearly black in some cases, in others it is a slight pallid grayish with a livid-violet shade, with many intermediate shades between the two; pseudoamyloid (Singer 1938) is a positive reaction if the final color obtained is brown to purplish brown in the spores, redbrown to wine red in the trama. In both cases it may be only one layer of the cell wall that reacts or adsorbs. Inamyloid walls are yellow to nearly hyaline. Naturally, the reactions of strongly pigmented spores and hyphae, at least the strongly pigmented layers of their walls, cannot be inserted in this scheme since the reaction, one way or another, would be obscured, and covered up by the pigment, and treatment of these walls with substances that in the end would extract or destroy the pigment, would also alter the initial reaction of the wall. Consequently the question of amyloidity and therefore the use of Melzer's reagent has originally been confined to hyaline or light colored (stramineous, palest melleous) tissues and spores, and to the colorless endosporia of pigmented spores.

This does not mean that differences in shade of spores treated in Melzer's reagent should not be taken into consideration if the spores are naturally strongly pigmented. Indeed, Smith & Singer, in their work on *Galerina* have been able to point out that such differences exist between species of that genus and similar observations are incorporated in the recent monographs of *Gymnopilus* by Hesler (1969) and *Pholiota* (Smith & Hesler 1968), and in notes on *Conocybe*, *Crepidotus*, and certain boletes (see especially Smith & Thiers 1971). However, the interpretation of the results is a great deal less immediate and easy than in the pale-spored species. As Smith & Hesler have correctly pointed out, only a comparison of spores in various media with those mounted in the Melzer reagent can lead to a correct decision since the pseudoamyloid spores show an appreciably more reddish tinge than the spores seen in other media whereas the inamyloid spores do not show a more reddish coloration in the Melzer. Even so, the results are occasionally not too encouraging since unusually weak reactions are often observed which in older herbarium material tend to gradually disappear. Singer (1961) has pointed out a fact of particular interest for type studies. The amyloid reaction of the spore walls as well as the pseudoamyloid reaction of the hyphal walls is well visible in even the oldest specimens of the Persoon Herbarium (L) and in spite of poor conservation (this does not hold for material conserved in alcohol and other liquids) whereas the pseudoamyloid reaction of the spores under ordinary conditions tends to become weak and finally nil in a majority of the spores after long preservation. An interesting observation by Singer on albino-spores of a *Psilocybe mutans* cultured by K. McKnight in Michigan should be mentioned here: The hyaline-spored form of the species showed distinctly pseudoamyloid walls while the reaction was rather vague in the normally pigmented spores.

Amyloid reactions, obtained in the ascii of the Ascomycetes, in the spore walls of the smooth-spored *Leucopaxillii*, in the exosporial ornamentation of *Leucopaxillus* (Pl. 63A), *Melanoleuca*, *Russula* (Pl. 13), *Lactarius* and *Bondarzewia*, and in the hyphae

of *Polyporus* are by no means equivalent to each other, or suggesting a similar chemical composition of these walls. Not only is the color obtained dissimilar (pure blue in the ascospores - pale livid grey to almost subhyaline in the smooth-spored *Leucopaxilli* - blackish violet in the exosporial ornamentation and some hyphal in crustations, bluish violet in some cystidia and the hyphae of the rind of the stipe - as opposed to pinkish amethyst to deep reddish brown, i.e. reaching a tone usually associated with pseudoamyloid reaction in the pseudoamyloid hyphal walls) but solvents and dyes also act in a different manner. Amyloid and pseudoamyloid reactions are clearly different in color in the spores of the Basidiomycetes, yet they sometimes intergrade almost unnoticeably in the hyphal walls. Amyloid reaction that is not of the amylose (starch) type becomes often pseudoamyloid in thick-walled hyphal walls and more amyloid in thin-walled hyphae or such hyphae where only a thin layer is iodine-positive. Locquin thinks that the exosporial ornamentation of the spores of the Russulaceae contains amylose which would almost certainly be true also for *Leucopaxillus* (warty-spored species) and *Melanoleuca*, and very likely also for the amyloid outer layer of some hyphae, especially the cuticular haphae of some species of *Chroogomphus* and certain Boletaceae. In these cases, the term "amylaceous" or "nearly amylaceous" is sometimes used in order to characterize the reaction in contrast to the ordinary amyloid reaction of the spores of *Amanita phalloides* or the rather pseudoamyloid reaction of the pilose epicutis of *Crinipellis*.

Amyloid spores and pseudoamyloid hyphae were discovered at approximately the same time (1887) by Patouillard (*Aleurodiscus vitellinus*) and Rolland (*Mycena tenerrima*) in the Basidiomycetes, and in other fungi and lichens amyloid reactions were known even before that. It was later found by Kühner (1938) that not only the hyphae of the stipe of *Mycena tenerrima* but all hyphae of the trama of most *Mycenae* are (pseudo)amyloid; he has later defined some sections in the genus *Marasmius*, and some of these sections, or parts of them, have (pseudo)amyloid hyphae. More species with (pseudo)amyloid trama were found later by Singer (*Pseudobaeospora oligophylla*; *Mycena violacea*, etc.). The author has also (1942) discovered epicutis hairs that are somewhat intermediate between amyloid and pseudoamyloid, more frequently closer to the latter (*Crinipellis*, *Chaetocalathus*; *Lachnella*).

Kühner and Maire have first indicated a large number of Lepiotas with an unusual red-brown reaction with Melzer's reagent which they interpreted as non-amyloid, but were later designated as pseudoamyloid by Singer\* who also indicated that aside

\*1938 (*Revue de Mycologie* 3: 191). Later Orton has proposed the term "dextrinoid" in order to replace the "less accurately expressive" term pseudoamyloid. Even if there were degrees of expressiveness involved, I do not feel that a widely used term should be replaced after 22 years unless it conveys a false notion or lacks in precision, or else can be replaced by a strictly chemical term. Should we now replace the term macrocystidia by "resinocystidia"? Even if terminology is not subject to legislation by nomenclature rules, should we not strive to maintain a certain continuity in scientific terms as well as in plant names? On the other hand "dextrinoid" is not any more expressive or accurate than amyloid or pseudoamyloid since both terms refer exclusively to some color changes and include even as such very different color ranges and supposedly reacting chemical substances; they are consequently liable to eventually be replaced by terms which have a chemical significance. It should be noted here that a third set of terms has been chosen by Heinemann (1973) who calls amyloid walls or layers metachromatic, pseudoamyloid ones orthochromatic, and inamyloid ones achromatic. Since the Melzer reagent is mostly registered as a reagent rather than a dye this usage may not be acceptable to all mycologists.

from certain genera related to *Lepiota*, especially those with spores that have a germ pore, and the genus *Pseudobaeospora*, pseudoamyloid spores also occur in the genus *Chaeotocalathus* (1942). Much later it was found that pseudoamyloid spores are present in *Hygrophoropsis* and *Paxillus panuoides*. Amyloid cystidia were first indicated by Bondarzew & Singer (Sov. Bot. 1943, p. 39), but in the genera *Geopetalum* (Pl. 2, 1) and *Gloiocephala*, Singer (1951, 1960) reported pseudoamyloid cystidia. One species of *Marasmius* has cystidia which turn olive grey in Melzer's reagent. Finally, O. Miller (1971) has also found mycelial elements giving a positive amyloid reaction in *Omphalotus*.

All students of agarics will readily admit, after they have given the iodine tests a fair trial, that this microchemical method provides characters that are of enormous importance in taxonomy if evaluated critically, and used with discrimination. This may not always be the case in other groups of fungi though it is certain that in the "Poriae" as well as other aphyllophoraceous polypores, and in the Hericiaceae, Auriscalpiaceae, Favolaschiaceae, to name only a few Aphyllophorales, and in *Secotium*, in many Hydnangiaceae, and according to A.H. Smith in *Rhizopogon* and *Mycolevis* to name some Gasteromycetes, positive reactions found in spores and/or hyphae have some taxonomic importance. In the agarics, this character must be used just as all other characters - cautiously applying it as a specific character in the beginning stages of the investigation, and eventually - after enough data have become available - the amyloidity may or may not turn out to be a sectional (*Dermoloma*, *Cystoderma*), a subgeneric (*Amanita*, *Fayodia*), generic (*Xeromphalina* et al.), tribal (*Panelleae*, *Leucopaxilleae*), or even family character (Russulaceae and Bondarzewiaceae). The same is true for pseudoamyloidity (generic character in *Lepiota* and all *Leucocoprineae*, *Crinipellis* and allied genera). There can be no methodical determination of agarics without Melzer's reagent and a careful study of its action upon the walls of the spores, hyphae and epicuticular elements.

It was Josserand's (1942) idea to remove the amyloid (interstratum) ornamentation with certain organic or inorganic solvents of amyloseous and amyloid substances or mixtures containing such. Locquin was more methodical about this (1943); the author refers to Locquin's paper on the subject because it appears that this method may have some influence on a future subdivision of the amyloid reactions on one hand, and on the introduction of the fundamental ornamentation in taxonomic mycology on the other.

Locquin, for this purpose, used nitric acid, zinc chloride (solvents of starch-containing spore walls), ammonium oxalate (for walls containing pectine compounds), NaOH and KOH (for wall containing hemicelluloses), and sodium hypochlorite (for chitin). Some of these reagents are also used in other micro- and macroscopical tests newly introduced into taxonomic mycology, especially in the Agaricales (but also in the Aphyllophorales, and with a great potential importance in the Gasteromycetes, and perhaps the Ascomycetes). We shall first review the microchemical tests:

Potassium hydroxide, KOH (which can be substituted by sodium hydroxide, NaOH), is used in *Cystoderma* (Smith & Singer 1945) since it darkens certain layers

of the covering of the pileus in certain species whereas this reaction is not noted in others. It has been found a valuable additional character. In fact, the main classification of the genus, in our monograph, is rightly based on two microchemical characters, amyloidity and KOH reaction. The pigments of *Callistodermatium*, straw color to deep spadiceous and incrusting the cell walls, is dissolved in alkali solutions (KOH and NH<sub>4</sub>OH) whereby it becomes violet. In some groups of *Crinipellis*, the epicuticular hairs become gray to green in KOH (Singer 1942). KOH also causes a green discoloration of the pigments in the trama *Anthracophyllum* (Singer 1944). A similar greening in alkali, both macro- and microscopically, can be seen in other Collybieae: *Collybia alkalivirens* Sing. (Singer 1948) and *C. semihirtipes* and *C. spongiosa* (Halling 1983); *Marasmiellus lysochlorus* and *M. potassiovirens*, *Neoclitocybe portentosa* Sing. and Marasmieae: *M. prasiosmus*, *olidus*, *copelandii* (Redhead 1982); *Crinipellis alkalivirens*, *mobilis*, and others.

In concentrated H<sub>2</sub>SO<sub>4</sub>, the spores of certain Coprinaceae change from black to pale livid whereas in others the same black or fuscous membranal pigment is resistant (Kühner 1929); this reaction has been used for the classification of the Coprinaceae by Singer (1936). Another taxonomically important reaction was that obtained with ammonia (NH<sub>4</sub>OH) on the internal body of the cystidia of *Stropharia*, *Naematoloma*, *Pholiota* (Kühner 1936); these cystidia were later distinguished from other (pseudo)cystidia of the Strophariaceae and the Agaricales as a whole by Romagnesi, under the name chrysocystidia (Pl. 17, 3). The author has found deep blue contents in cresyl blue mounts, and therefore thinks that the chrysocystidia are chemically - if not otherwise - related with the gloeocystidia inasmuch as they sometimes are found to communicate with tramal hyphae of the same chemical character and aspect (the chryso-vessels). The trama of *Xeromphalina caulinodans* and closely related forms turns red with ammonia (NH<sub>4</sub>OH) according to Singer (1936); this reaction is due to a transformation of the brown, incrusting pigment of the hymenophoral trama. Another group of species in this small genus does not show this reaction. Kühner (1935) has first noticed and used as a character in his *Galera* monograph, the needle-like crystals that are formed in preparation of the hymenium in various species of *Conocybe* whereas other species of the same genus do not form them. Singer (1937) reported the same long, colorless needles in ammonia preparations of the hymenophore of *Phaeomarasmius wieslandri* and has observed the same reaction on an alpine form of (or form related with) *Inocybe lacera*. This is the first chemical micro-reaction that is not a color reaction. NH<sub>4</sub>OH also gives a green reaction with the exudates of the (pseudo)cystidia of a certain group of species of *Psathyrella*, indicated by Kühner & Romagnesi (1953) and Singer (1969).

Several other microchemical characters have since then been added to the above, viz. the reddish pigment in the *Gomphidii* that shows in a formaldehyde-acid solution, and other characters based mainly on the solubility of fungus pigments. The widest application of microchemical reactions is now made in the Russulaceae where a mixture of aldehydes with strong acids is known to provoke a darkening of the contents of the macrocystidia, dermato-pseudocystidia, and some oleiferous hyphae and laticiferous vessels. The reagents used are:

*Sulfovanillin:*

Chemically pure vanillin	0.5 gr.
Distilled water	2.0 gr.
Pure sulphuric acid	<u>4.0 gr.</u>
Sulfovanillin	6.5 gr.

The resulting solution is of a deep rich yellow. It should be filtered through glass wool, or handled very carefully as the undissolved crystals and those that form after a while when the solution begins to disintegrate, often cover the section studied, and, under pressure, the cover glass may easily be broken. Sulfovanillin must be used on fresh material. It is true that the results are sometimes satisfactory with well dried material during a period of several months after collecting but they are no more conclusive if the reaction is negative.

*Sulfoformol:*

Formaldehyde 40 p.c.	
watery solution	6 cc.
Distilled water	3 cc.
Pure sulphuric acid	<u>10 cc.</u>
Sulfoformol	19 cc.

The resulting solution is colorless. It must be used on fresh material or on material that has been in formalin for not more than 6 months.

*Sulfobenzaldehyde:*

Same as sulfoformol, the formalin replaced by benzaldehyde.

*Chlorovanillin:*

Same as sulfovanillin, but the sulphuric acid is replaced by concentrated hydrochloric acid.

All four reagents (which this author has used for routine and photomicrographic work in the Russulaceae and "Astrogastraceae" since 1930, see Pl. 39) give parallel reactions:

Table II

Organs of the Russulaceae	Sulfo- vanillin	Sulfo- formol	Sulfobenzal- dehyd(e (or sulfo-para- dimethyl- amino benzal- dehyd)e)	Chloro- vanillin
Macrocytidia, dermato- pseudocystidia, some oleiferous and lati- ciferous vessels	blue	brown	black	blue
Cystidia, gloeocystidia, basidia, hyphae, ciliate dermatocystidia, prim- ordial hyphae	(hyaline to) rose color	hyaline	hyaline	(hyaline to) rose color

Sulfoformol has also been tested in the pseudocystidia of *Lentinellus* where it gives the same results as in *Russula* and *Lactarius*. All these reactions have been used on a large scale by R. Maire (since 1907). Sulfovanillin was introduced into lichenology by Lindt (1885), and in mycology by Arnould & Goris (1907). They are now generally used in *Russula*, *Lactarius*, and *Lentinellus*.

The author can indicate a number of dyes which can "replace" the aldehyde-acid reagents; but their use is not recommended because the reactions of the reagents are not fully parallel with the metachromasies of the dyes in question which will tend to stain deeper any banded or coarse granular contents in macrocystidia and often also other pseudocystidia.

A reagent particularly suited for the observation of the fine structure of spore and other wall layers, for example the endosporium of the Russulaceae - although less suited for routine taxonomic work - has been indicated by Locquin: Glycerin-mercurous-chloride (preparation and use see *Bull. Soc. Mycol. Fr.* 48: 172-174. 1952).

### *Macrochemical color reactions*

Macrochemical color reactions were first used for the determination of certain polypores. Müller (1872) discovered the violet discoloration taking place when *Hapalopilus nidulans* is exposed to ammoniac vapors. Harley (1896) discovered the deep violet discoloration of the pigment of *Lactarius necator* with alkali which can be used as an indicator - in acid solutions the same substance turns pale pink. This reaction is unique among the *Lactarii*, only *L. necator* and, according to the experience of the author, *L. atroviridis* show it. In the same year Bourquelot & Bertrand introduced guaiac, whose reaction with fungous tissues had been discovered by Schönbein (1856), into general use in the Agaricales, and in 1907 Arnould & Goris initiated the use of sulfovanillin in *Russula*. Since then some authors continued to study the action of chemical reagents on the various parts of Basidiomycetes, especially agarics (Bataille, R. Maire, Barlot, Kühner). But reagents did not become routine tests in any group of Agaricales until Melzer & Zvára (1927) introduced a whole series of chemical reactions and at the same time used the reactions for taxonomic purposes; in fact, the subdivisions of *Russula* in Melzer & Zvára's monograph are almost too much based on chemical reactions. In 1938, J. Schaeffer & Möller introduced the use of several chemical characters in the taxonomy of the genus *Agaricus*, and in the same year, chemical characters were first used in the Boletaceae and Gomphidiaceae by Singer, and new reagents were added to those already used in *Russula* and *Lactarius* by Heim. Also in 1938, the first general survey of the reaction of guaiacol was made by Singer, and it was shown that even in *Russula*, the genus for which it was first introduced, the reactions are constant in some species, and inconstant and unreliable in others. At the same time, the author used chemical characters for the delimitation of genera, and in phylogenetic problems, and so did other authors (Heim, Romagnesi). In 1939, Bousset recommended the use of monomethylparamidophenol for chemical

tests of Basidiomycets, and his findings were supplemented by numerous tests of this particular reagent in the author's papers, and he as well as other authors widened the scope of application of Melzer & Zvára's reagents beyond the genus *Russula*. Especially  $\text{FeSO}_4$  and  $\text{Fe}_2\text{Cl}_6$ , phenol and formaldehyde have become standard reagents for the laboratory and even for extended field trips. Henry and all modern specialists of *Cortinarius* make use of these and other chemicals in their work on *Cortinarius*; Singer on *Paxillus*; Konrad & Josserand on *Collybia*, etc.

This is in short the history of the macrochemical color reactions up to 1949. The tendency to use these characters has rather increased than decreased since then.

The following is a list of the most important chemical reagents, the reactions obtained and the genera in which they are used most frequently:

### 1. Reagents of oxydases:

*Guaiac*. Ordinary guaiac tincture; the oxydases present in fungi act on the guaiacconic acid present in the resin, if atmospheric oxygen is present. A blue (or green) to purple spot is formed on the surface of the section through the stipe in all those agarics and boletes that react positively. The reaction can be used in all genera. The time necessary to obtain the first result should be noted. Indispensable in *Inocybe*.

*Guaiacol*, watery solution, slightly below the saturation point. Reaction, if positive, from salmon-color-orange to rose color or bluish pink, slowly darkening to dark copper or chocolate color in most cases; the base of the stipe is always most sensitive; the reaction is useful in the Russulaceae, Tricholomataceae, Amanitaceae.

*Pyramidon* in saturated, watery solution. In species with positive reaction, the context of the stipe becomes light lilac color. It is used only in *Russula* and *Tricholoma*.

### 2. Other organic reagents:

*Phenol (carbolic acid)*, 2 p.c. watery solution; reaction either negative or positive; if positive, it is chocolate color, or deep purplish violet after 20 minutes; in some cases the reaction is more sordid grayish vinaceous, reddish, etc. If after 20 minutes no distinct reaction has taken place, the reaction is called negative, even though it may show up after an hour (Amanitas of the *phalloides* group). Indispensable in *Russula* especially the mild tasting species, *Amanita*, especially the exannulate and the amyloid-spored groups, in *Leccinum*, also used in the Tricholomataceae generally, and in *Lactarius*.

*Formaldehyde (formalin, formol)*, 40 p.c. watery solution; reaction varies; it usually is positive in such species that have a tendency to change the color of the context by autoxydation, yet, at times it may act in the opposite way, inhibiting the autoxidation. This is also a slow reaction, and sections treated with formaldehyde should be observed at least 20 minutes. This reaction is indispensable in *Russula*, *Tricholoma* (the clampless group), *Gomphidius*, *Leccinum* and other boletes.

*Aniline (aniline oil and aniline water)*. This is either pure aniline oil, or the "oil" mixed with an equal volume of distilled water. Since 1932, aniline oil is used almost

exclusively. It becomes red to copper red on wounds of the stipe of mature *Russula xerampelina* and allied species, and is more or less parallel in its reaction with that of ferric sulfate. It is also specific in certain cases with the lamellae of the Russulaceae where it causes a central stained spot and then a bluish gray or green zone around it (especially important for *R. emetica* and allied species). Also occasionally used in other groups, e.g. boletes, *Agaricus*, and, among aphyllophoraceous genera: *Albatrellus ovinus*. In Russulaceae, especially on the lamellae, the reaction is slow.

**Cross reaction:** This was described by J. Schäffer and Möller, and consists in a test made on the surface of the pileus of the species of *Agaricus* whereby a transversal streak with  $\text{HNO}_3$  is made, and then crosswise, another streak with aniline oil. The result, if positive is an orange red to fire red discoloration. It must be considered, however, that the two substances often react with each other without interference of the *Agaricus* whereby a brightly colored crystallized mass is formed that may be misleading. Watling (1971) emphasizes that the aniline must be a clear straw colored liquid rather than a deteriorated, impure reagent.

**Phenol-aniline.** This consists in the mixture of a few drops of aniline with phenol (2 p.c. watery solution). While all the preceding reactions have to be performed with fresh material, never with dried or otherwise prepared material, this reaction is recommended by J. Schäffer for dried material of *Russula*. The reaction is from nil to nearly black after prolonged exposure.

Lactophenol gives a dark red reaction with some Boletaceae and Schiff's reagent a red-violet to blue one with certain agarics.

**Sulfovanillin, sulfoformol, sulfobenzaldehyde and chlorovanillin.** The formulas are the same as those given under microchemical reactions. For macrochemical color reactions, the first and the last of these reagents are preferred. They are used mainly for the identification of certain *Russulae* (*R. rosea*, *R. minutula*, *R. albida*, etc.) in which the context of the stipe and, especially, the surface of the stipe, with sulfovanillin immediately turn very bright red and remain that color (Pl. 1, L6, becoming Pl. 2, L6, then Pl. 3, L6, finally Pl. 4 L6); any stain less bright red, such as "Tommy red", "Red Cross", or even more purple or carmine, or tending to brown or blue, and soon disappearing or becoming very deep colored, is considered negative. With chlorovanillin, the difference between positive and negative is even more conspicuous (the negative reaction being not deeper than "baby rose", "candy pink", "coral", "confetti"). The reaction with *R. albida* is not quite so striking as that with the two red species. All color indications are in Maerz & Paul terms. Sulfovanillin has also been used (by Kallenbach and Romagnesi) for Boletaceae but its use in that family is hardly justified since the reactions are those of sulphuric acid. Sulfoformol is used for these same *Russulae*, that turn red with vanillin, and also, according to Bataille, with *R. luteotacta*, *R. rosacea*, *R. queletii*, and according to Singer, with *R. anomala*.

**$\alpha$ -naphthol.** A scalpel tip full of the reagent is dissolved in about 2 ccm of 90 p.c. alcohol, and then 4 ccm water are added. The solution reacts almost uniformly with the context of the stipe of *Russula* causing a deep indigo to violet blue discoloration

after a few minutes. Some species react very slowly, perhaps not at all. It would be interesting to know what results - if any - can be obtained in other genera.

*Pyrogallol*. A 5 p.c. watery solution is said to give richly colored (yellow to brownish yellow) reactions with the context of the *Russulae*.

*Monomethylparamidophenol* ("methol"). The crystallized reagent, often used in photography, is dissolved in about 20 times its weight of distilled water; the solution is used immediately since it is unstable. The positive reaction varies from a pale sordid lilac or lilac ("vinaceous purple" of Ridgway, or more sordid), finally reaching "dark nigrosin violet", "deep naphthalene violet", "blackish purple", "taupe brown", etc. The reaction sometimes passes through pink or salmon, and sometimes through blue (*Lactarius volemus*), and at times becomes arrested at these colors. In other cases a more yellow reaction is observed which is probably of another chemical nature than the violet one which is obviously due to the fact that the fungus tissue contains some substance that yields oxygen to the reagent. The same capacity as reducer may also prevent the autoxidation that takes place in the bluing Boletaceae when monomethylparamidophenol is added before the discoloration of the context starts. The negative reaction is neither preventing any natural discolorations, nor does it show any pink, salmon, blue, violet, or yellow discoloration provoked by the reagent itself, and the darkening that is often seen after a very long time is rather due to a transformation of a different order than to the reaction called "positive" here. The reaction is variable with a large number of species, but with others it is quite constant, and a variable amount of time (1-30 minutes) is required to reach the different stages of the reaction. This difference in time is perhaps more important than differences in shade which do not seem to be very constant. The reagent must be applied on fresh, mature, not watersoaked material. It gives good results in many groups, almost uniformly - as far as limited experiences allow to state - in Russulaceae (weak reaction in *Russula fellea*) and *Lyophylleae*. It is, generally speaking, more valuable in white-spored agarics than in dark-spored groups and in the boletes.

*Methylchlorantimoniate* (in methylalcohol-solution) is a reagent designed to translate the acrid taste of the Russulaceae into an optical character. The positive reaction is lead gray, the negative reaction is unchanging (or belatedly becoming slightly bluish) context.

*Ethylchlorostannate* (alcoholic solution) is said to give a yellow-brown reaction with *Amanita gemmata* under the cuticle) whereas all other species examined in this genus are completely negative.

*Sulfobenzene-para-diazonium chloride* (for *Russula* and Boletaceae) and benzidine (di-para-diamino-benzidine) (for *Tricholoma*, *Agaricus*, Russulaceae, Paxillaceae, Boletaceae et al.) give various-colored reactions whose value in mycology has been corroborated by Micka (1954) and Micka & Klán (1980). Clémenton (Schweiz. Zeitschr. f. Pilzk. 47: 12-13. 1969) has shown that o-toluidin (dimethylbenzidine, dissolved in 95% alcohol) can advantageously substitute for benzidine as the latter is cancerogenic in man. However Micka & Klán find o-toluidin less versatile than

benzidine since two reaction sides in the molecule are blocked by the methyl groups. They use 0.5 g benzidine dissolved in a warm mixture of 5 ml acetic acid with 5 ml water, and then water was added to reach a total volume of 50 ml.

All these new data show that there is still room for more organic reagents to be used in the taxonomy of Agaricales. The same impression is conveyed by Sandor's (*Zeitschr. f. Pilzk.* 22: 97. 1956 and 25: 76, 111. 1959) suggestions.

More tests with more species are needed in order to corroborate the taxonomic importance of stains not mentioned above, but found listed in the mycological and microbiological literature (see also list of reagents in Booth's *Methods of Microbiology* 4: 572-577).

### 3. Iron salts:

$\text{FeSO}_4$   $\text{Fe}_2\text{Cl}_6$ , and ferric alum can all be used for the same purpose, the first of them being the most commonly used, in 10 p.c. watery solution, on fresh mature specimens. The discolorations are of several categories (1) none, i.e. negative reaction - no color change, or color change indistinct; (2) some kind of olive, green, blue-green, blackish-green discoloration of the context of the stipe - often also the surfaces. This reaction is widely distributed in agarics and boletes, especially in *Russula xerampelina* and related species, *Lactarius volemus* and related species, some *Russulae*, *Compactae*, some species of *Tricholoma* and *Tricholomopsis*, many *Cortinarii* and other dark-spored agarics, many Boletaceae, *Gomphidius*, etc. In the genus *Gomphidius*, the reagent differentiates the presence of a chemically distinct subhypodermial layer. (3) All gradations from a rather pure pink or salmon color to sordid gray with or without a slight mixture of reddish. This is the ordinary reaction with the Russulaceae, with *Tricholoma albobrunneum*, and other agarics. (4) Blue or green-blue to slate gray. This reaction is commonly found in *Leccinum* where the gradation between blue and gray is of taxonomic importance; also in other boletes. (5) A violet reaction is characteristic for *Lyophyllum connatum* (lamellae). (6) A variable color effect on the cuticle of the pileus (e.gr. *Russula ferrotincta*).

### 4. Ammonia:

Ammonia vapors ( $\text{NH}_3$ ) and ammonium hydroxide, concentrated solution ( $\text{NH}_4\text{OH}$ ), are both used. They must be used on strictly fresh specimens, on all organs separately. The color effects are very varied, and often differ in different organs as well as with the age of the carpophore and temperature (specimens that had been exposed to freezing temperatures sometimes react differently). The most valuable results were obtained in the Boletaceae, Gomphidiaceae, Paxillaceae, Cortinariaceae, and Agaricaceae, but also with some genera of the Tricholomataceae, with *Russula* and *Lactarius*.

### 5. Strong alkalis:

Potassium hydroxide ( $\text{KOH}$ ), 15 p.c. solution in water (some use 10 p.c.), and sodium hydroxide ( $\text{NaOH}$ ), same concentration, act in the same way in all cases known to the author. KOH is a standard reagent for all groups of Agaricales used in fresh and in dried specimens separately, on all organs separately. The action can

often be reverted at a given pH by application of a diluted acid, and certain pigments of Agaricales (*Lactarius turpis*, *L. atroviridis*, *Collybia iocephala*) are good indicators. KOH as a reagent, specific for certain species or groups of species, is indispensable in the Boletaceae, *Agaricus*, *Amanita*, *Leucoagaricus*, and *Cortinarius*. The action is almost instantaneous.

#### 6. Strong acids:

Sulphuric acid ( $H_2SO_4$ ), concentrated. Used on fresh specimens of *Amanita*, also on boletes, some Tricholomataceae, *Gomphidius*, *Cortinarius*, *Agaricus*, *Lepiota*, *Leucoagaricus*, etc. Less important than KOH, this reagent must be used on fresh specimens. The action is instantaneous or almost so.

Hydrochloric acid (HCl), concentrated, used as above.

Nitric acid ( $HNO_3$ ), concentrated, used as above.

Those who go beyond the verification of data already available, by testing thus far untested species, or species whose reactions have not yet been published, will do well to adhere closely and consistently to the formulas, and also to constant and equal conditions and methods. It is also extremely important to avoid painstakingly interference between different reagents. Phenol and aniline can never be used on the same carpophore, and without the utmost cleanliness. Ammonia vapors should be kept from other reagents, especially  $FeSO_4$ . Young specimens should not be taken into consideration, or only for the sake of comparison with adult specimens. Generalizations should be made only after a long experience with the species in various ecological conditions, and with the behavior of the reagent under various chemical influences. The colors obtained should be indicated in color chart terms wherever this appears to be advantageous.

7.  $AgNO_3$ , silver nitrate (1 g  $AgNO_3$  in 10 ccm  $H_2O$ ), used by Moser (1960) for *Cortinarius*, was shown to be taxonomically useful also in other groups of Agaricales. So was  $HgNO_3$  and other salt solutions.

#### *Chemical analysis of the carpophores*

The use of chemical analysis of the carpophores of the Agaricales has aroused justified hopes for the taxonomist. Tyler - who himself has contributed many new taxonomically valuable data, quotes Hänsel\* as saying that "to take without further evidence either the sporadically or ubiquitously occurring compounds as a guide to plant classification would be just as artificial as the attempts at classification based solely on leaf form or the number of stamens". However, some of the data now available seem to go far beyond sporadic or ubiquitous occurrence and have already influenced the taxonomy of the Agaricales in certain instances, justly so in my opinion, while others are mentioned here in spite of the sometimes still fragmentary surveys published because they show promising possibilities for further research, as soon as more taxa have been analyzed.

\*Hänsel, R. (1956) Pflanzenchemie und Pflanzenverwandtschaft. *Arch. Pharm.* 289: 619-628.

In this category belongs the demonstration of the formation of cyanic acid by certain agarics. In order to become more conclusive, the list of agarics known to produce HCN beyond a certain minimum amount (according to the sensitivity of the picric acid method), should be supplemented with a list of the species that under these circumstances do not show any appreciable formation of HCN. More than half of the species indicated by various European authors\* have been checked by this author on material from the United States, and the result was positive in every case. This points to a strong specific constancy of this character, and the comparative simplicity of the method of qualitative demonstration of cyanic acid in agarics makes it possible to use it more extensively than is done at present.

Quantitative analyses of certain specific carbohydrates, acids, etc. are also useful in taxonomy though they cannot be expected to become routine tests for determination. For instance, Heim & Romagnesi (1934) referred to the analyses that were made on a rather large (yet still insufficient) number of Agaricales in regard to allantoic acid. Heim & Romagnesi found that the high percentage of this acid present in *Coprinus* and *Leucocoprinus*, as against a low percentage in *Macrolepiota*, shows a certain chemical affinity between *Coprinus* and *Leucocoprinus* and increases the hiatus between *Leucocoprinus* and *Macrolepiota* on the other hand. These data are based on a paper by Fosse & Brunel (1933).

Frèrejacque (1939) published a list of species which he had studied as to their contents in mannitol. He states that the list is not complete enough to make final conclusions. But it is obvious that the figures representing the weight of mannitol per 100 g of the dried carpophores keep in definite limits characteristic for certain groups of fungi. So we find a medium high to high percentage of mannitol in *Gomphidius* (which is thus chemically separated from the other black-spored agarics), *Paxillus*, and boletes (both related to the Gomphidiaceae and often

\*The last complete list published is that of Langeron, *Précis de Mycologie*, Paris 1952. With one species indicated later (Singer 1953) and another by Heinemann we obtain the following list:

- Geopetalum carbonarium;*  
*Pseudoclitocybe obbata*, *P. cyathiformis*;  
*Clitocybe alexandri*, *C. fragrans*, *C. gibba*, *C. parilis*, *C. geotropa*, *C. nebularis*;  
*Collybia dryophila*, *C. butyracea*, *C. "hariolorum"*, *C. maculata*;  
*Lepista nuda* (see Guyot 1917; this has not been verified by other authors);  
*Pleurocybella porrigena*;  
*Leucopaxillus giganteus*;  
*Marasmius globularis*, *M. oreades*, *M. pampicola*, *M. rotula*;  
*Melanoleuca melaleuca*; *M. cognata*;  
*Phaeolepiota aurea*;  
*Rozites caperata*.

Most tests have been made with the picric acid method which consists of the following procedure: the specimens are, in strictly fresh condition, cut into fragments and inserted in a glass vessel that can be closed nearly airtight (exsiccator). A piece of filter paper (2 × 20 cm) is immersed in a solution of picric acid (1 p.c.). After the paper has dried, the same paper is immersed in a solution of 5-10 p.c. of sodium carbonate (repeat this operation several times, leaving the paper in the NaCO<sub>3</sub> solution several seconds every time). The paper is then hung riding on the rim and the vessel closed firmly. The paper outside remains yellow; the paper inside becomes slowly (over night) dull red if the fungus exhales HCN. Another method is that of Schönbein, another that of Deniges (the latter apparently the most sensitive).

combined with them in the suborder Boletineae); in the natural group of *Lactarius* and *Russula*, he indicates a medium to usually high percentage of mannitol, with *Russula delica* showing a more than twice as high percentage than *Lactarius vellereus* (which might be used as a correlated character in addition to the absence of latex and the intermixed hymenophoral trama in the former). There is also a rather high percentage of mannitol in *Agaricus* and *Leucoagaricus* whereas in *Lepiota* it is abruptly very low. This would tend to show chemical affinity between *Agaricus* and the white-spored Agaricaceae. In the Tricholomataceae, the figures are low to rather high (up to 10% in *Armillariella mellea*) and in all other groups tested by Frèrejacque consistently low, reaching zero in *Inocybe maculata*.

A large number of facts, many of them concerning the Agaricales, have been assembled by I.A. Pastac (1942) on the coloring matter in fungi but this interesting survey which has been useful for those concerned with fungus chemistry, shows that the accumulation of data had, at that point, not arrived at a level where they could have influenced taxonomy. But later taxonomically useful contributions were made by Fiasson & Arpin (1967), Hegnauer (1962), Arpin (1967) and Arpin & Fiasson (1971), especially on the groups where carotenoids could be demonstrated to exist; and by Gabriel (1962, 1965) and Edwards et al. (1967), Steglich et al. (1966-71), Bresinsky & Orendi (1970), Bresinsky & Bachmann (1971), and Bresinsky & Rennschmid (1971) for "boletol"-like substances in Gomphidiaceae, Paxillaceae, Boletaceae. As for the Cortinariaceae, valuable work, first suggested by Kühner (1949) and Singer (1951), has been done by Gabriel (1960-1965), and emended and interpreted taxonomically by Steglich & Austel (1966), Lösel & Austel (1969), Gruber (1970) and Moser and collaborators (in several recent papers) so that gradually the important first steps concerning the topography of the pigments (Kühner 1949) could be supplemented by chemical analysis of the pigments (see also the survey of the status of chemo-taxonomical work in the Cortinarii by Arpin & Fiasson in Petersen 1971). The results of these contributions will be discussed in the respective groups where they are of great significance and often serve as indicators of affinity among the genera and even higher taxa of Basidiomycetes, or, like Eugster, Frauenfelder & Koch on *Russula*-pigments, for infrageneric taxonomy.

Some authors (especially Bourquelot) have given special attention to the presence of oxidases, laccase and tyrosinase in fungi and results of tests for enzyme activity have been published since then, both for carpophores and mycelial cultures. In the Agaricales we do not dispose of lists large and detailed enough to influence taxonomy with the exception of the papers by Nobles (1958, 1965, 1971) which are invaluable for the understanding of the position and affinities of the Polyporaceae (see also p. 66).

The presence or absence of psychotropic alkaloids (psilocybin, psilocin) has undoubtedly some taxonomic importance in the darkspored agarics (Strophariaceae, Coprinaceae, Bolbitiaceae), where it is linked with the activity of certain enzymes which contribute to the oxidative transformation of psilocin to the blue (melanin-like) product first recognized as characteristic for the hallucinogenic species of that group by Singer (1958). The dephosphorylation of psilocybin is triggered by

phosphatase which leads to psilocin. Thus, according to Tyler (1971), the separation of *Copelandia* from *Panaeolus* is justified on chemotaxonomical grounds. On the other hand, it is futile to argue that all agarics containing psilocybin or psilocin should *eo ipso* be related, or that a certain sequence of reactions such as the alcaloid's transformation to a blue pigment is necessarily characteristic for a single genus or family. This latter phenomenon has also been recently observed in a fungus determined by me as *Gymnopilus purpuratus* (Singer 1969), obviously cortinaceous and seems to be shared by a number of other species of that genus, and at least one species of *Inocybe* and *Pholiota*, also by some secoziaceous fungi.

The taxonomic relevance of polyacetylene production in the Compositae has been shown by Sørensen, Bruun, Holm and Sørensen, but only 1963 was it introduced (Anchel, Silverman, Valanju and Rogerson) in mycology. Diatretyne 3-chromaphore, authentic diatretyne 3, diatretyne nitrile chromaphore, authentic diatretyne nitrile, diatretyne amide chromaphore and authentic diatretyne amide were shown to exist in various representatives of the Agaricales (253 species tested), and none in other families of Basidiomycetes (385 species tested). The diatretynes had first been observed by Anchel (1958) in co-occurrence (amide and nitrile) in *Clitocybe diatreta*, and the diatretyne producers have now been listed according to Dennis' classification (Dennis, Orton & Hora 1960) and this author's classification (first edition of the present work, 1951). The authors cited above (1963) came to the conclusion that in the latter system of classification the distribution pattern of the diatretynes appears more orderly since all diatretyne-producing species with one or two exceptions (*Psathyrella* species) fit into the family Tricholomataceae. The authors conclude correctly that "diatretyne production offers an additional characteristic, a biochemical one, in support of Singer's classification."

This conclusion might well apply likewise to the present author's earlier comments on the distribution of the antibiotics in Agaricales - frequently concurrent with modern taxonomy based on anatomical and cytological as well as physiological (ectomycorrhiza!) characters\*).

Furthermore it was suggested\* that the presence or absence of urea accumulation in the extract of certain Tricholomataceae might be a useful supplement to the standard observation by mycologists on the generic level since the lack of urea seems to be characteristic for the genus *Tricholoma*. This procedure appears to be applicable generally to the taxonomy of Higher Basidiomycetes as can be deduced from a list of chemotaxonomic results published by Tyler, Benedict & Stuntz (*Lloydia* 28: 342-353. 1965) whereby it was shown that the true Clitocybes show high percentages (but see also Harmaja (1969) and p. 237 of the present work) whereas, on the other hand, the split groups formerly lumped with the genus *Clitocybe* e.gr. *Laccaria*, *Omphalotus*, *Armillariella*, *Gerronema* (listed as *Omphalina luteicolor*) and *Hygrophoropsis* were negative. On the same ground, any conclusions regarding

\*Singer, Proceedings of the Seventh International Botanical Congress Stockholm 1950, p. 401-402. 1953.

\*Benedict, Tyler, Brady & Stuntz, Preliminary chemotaxonomical appraisal of certain Tricholoma species. *Planta Medica* 12: 100-106. 1964.

affinity between the Russulaceae and Hydnangiaceae with *Melanoleuca* should be discarded. The same approach offers interesting data as for the delimitation of *Galerina* vs. *Cortinarius*, Psathyrelloideae vs. Panaeoloideae, *Lyophyllum* vs. *Tricholoma* and for the infrageneric taxonomy of *Amanita*, *Stropharia*, *Entoloma* (see also Largent & Benedict 1971, and his treatment of rhodophylloid fungi under *Entoloma*, *Suillus*, and possibly *Pleurotus*, *Collybia* and other genera.

A detailed chemotaxonomic study of the chemical constituents has been carried out with regard to 39 species of *Inocybe* by Robbers (1964), taking into account 28 organic constituent substances. This has been shown to be of value for the infrageneric taxonomy of the genus. A less detailed but likewise very interesting study was carried out by Benedict, Tyler, Brady & Stuntz regarding the species of the complex *Tricholoma-Lepista-Tricholomopsis-Clitocybe* (1964).

In *Amanita*, the two principal subgenera distinguished by Singer (1950, 1951), the amyloidity of the spores, smoothness of the margin, and the occurrence of *Amanita*-toxins were indicated as correlated characters, a distinction which has been further corroborated by the latest studies on the *Amanita*-toxines (all in the group with amyloid spores) and alkaloids (most in the group with inamyloid spores) as becomes evident from the chemical and chemotaxonomic literature (Tyler, and collaborators, 1961-1963, 1966, Wieland 1968), with the exception of the fact that Tyler & Gröger (1964) found that *A. citrina* and *A. porphyria* are different from the rest of their group by the presence of relatively large amounts of tryptamine derivatives including bufotenine and serotonin. On the other hand, here too it should be emphasized that the mere presence of identical substances in two organisms should not be construed to mean necessarily that they are related. Tryptophane derivatives are widely distributed in plants and animals (bufotenin was first isolated from toads), and  $\alpha$ -and  $\beta$ -amanitin has been found in *Galerina*. It should be added here, that aside from toxic substances the amino-acid patterns and the urea-accumulation in carpophores are also taxonomically useful as suggested by Tyler and collaborators (1961, 1965).

In the words of Tyler (1971) "the genus *Agaricus* should prove to be a very fertile field for chemotaxonomic investigation", particularly in view of recent work on amino-acid pattern.

#### DNA-Analysis

Among the most promising modern approaches is DNA analysis. The highly sophisticated analytical work has thus far been satisfactorily accomplished only once, on the specific level, and only for a small number of Strophariaceae, in a very interesting dissertation by Klaus-Dieter Jahnke (Georg-August-Universität zu Göttingen 1984). It is hoped that the author (or other authors who will refine their method to the degree achieved by him) might in the future extend their investigations to the sectional and generic level.

Most coherent data available are useful on the specific level in Agaricales taxonomy, but will also be useful as confirmation of delimitation of sections when more data on more species are available. On the generic and higher levels - the subject mostly treated in the present work - we have too few reliable data at hand, and the data published often seem to be irrelevant for that very reason. Thus, the fact that in the Agaricales tested the characteristic band at Rf 0.5 is present except in *Lentinus* and *Flammulina*, leads Blaich (in Clémenton, *Bibl. Mycol.* 61: 220. 1977) to the conclusion that according to their aminopeptidase pattern "*Flammulina* and *Lentinus* seem to belong to the Polyporaceae".

## XX. PHYSICAL CHARACTERS

It has been suggested (but never realized in experiments) to compare the specific weight of dried carpophores\* and make tests on their elasticity. These tests are almost impossible to translate from speculation into reality. The specimens vary too much in different ages and under different climatic conditions, habitat conditions, and by intraspecific variation - as every mushroom grower will readily confirm. Another approach is that of provocation of luminescence by application of polarized light and Wood's light on various fungi, and the conclusions are though neither too encouraging nor too disillusioning, in any event worth the attention of the taxonomist. Josserand and Nétien think they have found another difference between *Russula* and *Lactarius* in the behavior of the carpophores in Wood's light, and this recalls a similar attempt, still unpublished, I believe, by Zuderell, Cernochorsky and Singer, with polarized light, where the most striking effects of luminescence were obtained with *Russula*, whereas the *Lactarii* remained almost dead. For more detailed evaluation of these results the reader is referred to the authors of the paper cited above (*Bull. mens. Soc. Linn.*, Lyon, reprint, p. 1-20).

Recently Harmaja (1969) has used ultraviolet light on dried specimens of *Clitocybe* with a view at utilizing the visible light-effect for the infrageneric taxonomy of that genus. It is obvious that certain subsections (or sections) can be distinguished using this as a correlated character.

Certain Macromycetes are capable of producing carpophores which often or regularly, while expanding, grow around and envelop foreign bodies (living or dead branches, culms, leaves, but also inorganic material). This phenomenon is called haptomorphosis. It has been studied experimentally by Nuss (1980), in relation to polypores. These experiments are undoubtedly meritorious, but they did not sufficiently elaborate on environmental factors which obviously influence their outcome. Hilmer (1982) observes that *Pleurotus ostreatus*, too, in its natural habitat is capable to grow around foreign bodies and that this character may be confined to solitary carpophores when the spore dissemination must be protected. Similar

\*And *Boletus torosus* has been characterized by particularly high specific weight of the fresh carpophore.

observations can be made in other families of Agaricales. It is therefore certain that haptomorphosis cannot serve as a character separating Aphyllophorales from Agaricales, or "agarics" from "polypores". But even if haptomorphosis were a useful tool for the taxonomist on a lower level, it must be kept in mind that it is necessary to extend Nuss' method by introducing a series of different growing conditions in each case and study a much larger number of species than has been possible until now.

## XXI. CYTOLOGICAL CHARACTERS

### *Nuclear cytology*

Cytology in the wider sense is now frequently applied in the taxonomy of the Agaricales; it has even found its way into the basic keys for determination in monographs as well as in surveys of genera.

The number of chromosomes has not yet been used by systematists; it seems to be generally rather low, and differences in shape apparently do not exist, or have not been brought to the attention of the taxonomists.

The nuclei, as a rule, are small, and their number in the mycelium, the hyphae of the carpophore, cystidia, basidia, and spores differs according to races, species, or larger groups of species or genera. This whole problem cannot be studied without due consideration of the whole life cycle and sexuality of the Agaricales whereby certain types and aberrations from the normal form will be considered separately, with their taxonomic application in view.

The most important basic contributions were made by Maire (1900-1902) and later Kühner (since 1926). Many other authors have contributed important details without, however, attempting to evaluate them for taxonomic purposes.

Summing up what is generally considered as the "normal" life cycle of an agaric and bolete, we shall start with a uninuclear spore that after germination gives rise to a haploid monocaryotic mycelium (also called primary mycelium, a term that should be abandoned). The septa between the hyphae of the haploid mycelia are clampless (except for a very few reported cases of "autodiploidization").

The spores as well as the primary mycelia resulting from them are sexually different, therefore the "normal" type of Agaricales comes under the group of so-called heterothallic thallophyta. Heterothallism in fungi was discovered by Blakeslee (1908) and in the Agaricales by Bensaude (1918). The sexuality of the heterothallic Agaricales appears in two forms, one of which is called bipolarity, and represents the usual bipolar isogamy among the representatives of this group, and another that was discovered by Kniep (1922) in which the mycelial descendants of a carpophore are physiologically divided in four instead of two groups, according to the schema:

	M 1	M 2	M 3	M 4
M 1.....	-	+	-	-
M 2.....	+	-	-	-
M 3.....	-	-	-	+
M 4.....	-	-	+	-

This means that in the bipolar forms, of the two physiologically different types of mycelium, each can copulate with the other type, whereas in the tetrapolar type, a mycelium of the type 1 can copulate only with a mycelium of the type 2, and a mycelium of the type 3 can copulate only with a mycelium of the type 4. In other words, we have here a form of sexuality with four sexes instead of two, a fact that made it necessary to emend the conception of sexuality (this is Quintanilis's opinion - but compare H.S. Jackson, *Trans. R. Soc. Canada* 38: 4-5. 1944).

The study of the copulations is technically achieved by single spore cultures\*.

After the copulation of two mycelia of the haploid generation, the second generation, normally the more important one in the Basidiomycetes (because the carpophores are usually produced by it), begins with the formation of the dicaryotic (secondary) mycelium, or the mycelial phase of the dicaryophyte immediately starts the formation of clamp connections and the cells consistently contain two nuclei which divide at the same time and pass into the new cell in a rather complicated way that is reminiscent of (and according to most contemporaneous authors homologous with) the similar hook-formation of the ascogenous hyphae (Ascomycetes). One nucleus of the pair resulting from the division of one nucleus of the original dicaryon enters a bulge that points outwards and backwards at the place where the new septum will be formed. The bulge - called clamp now - fuses with the parent cell, the double wall becoming dissolved, and the nucleus that was in the bulge enters the parent cell. At the same time, between the two nuclei of the second pair resulting from the division of the second nucleus of the original dicaryon, a new septum is formed inside the old hyphal cell, separating the new cell from the old one and thus leaving one nucleus of each pair in each cell. The two in the old portion and two in the new cell are now separated from the clamp by the laying down of an additional septum. The resulting structure, characteristic for the Basidiomycetes, is called a clamp connection (Pl. 27; 58, 1ch; 2ep). These clamp connections are normally present on all or almost all hyphae of the whole dicaryophyte, including the carpophore. The dicaryotic mycelium contains two nuclei in each cell because, after the fusion of two haploid mycelia with opposite polarity, the nuclei - though entering the same hyphae and remaining in pairs all through the dicaryophyte phase - generally do not fuse to form a diploid single nucleus. Thus reduction division is postponed throughout this generation and finally takes place in the basidia of the carpophore\*\*. Normally, only the dicaryotic mycelium is able to form carpophores. The hyphae of the carpophore and also the basidioles are typically binucleate (Dangeard 1895). The reduction division is usually followed by one or two more

\*As for methods, we refer to special papers, especially by Vandendries, and Lamoure (see bibliography).

\*\*Falck (1902) calls the carpophore phase of the dicaryophyte - tertiary mycelium, an unnecessary and misleading term that must be abandoned.

divisions which take place in the upper part (club) of the basidium, and the spindles of the first two, or at least the second division are in an obliquely subhorizontal or in an almost horizontal position, the spindles of the second division often forming an X-shaped (chiastic) figure. This is in contrast to the stichobasidial type in which the figures of this division are found one beneath the other in a more nearly vertical position and at a lower level of the basidium. There are probably what may be termed transitions between the basic types - chiasto - and stichobasidia - but not normally on the level of the Agaricales, nor, for that matter in the holobasidial Aphylophorales (excluding the Exobasidiales), where both types occur in otherwise rather closely related forms such as the Clavariaceae sensu lato and the Cantharellaceae sensu lato, and in the Gastromycetes where the basidia are normally chiastic. After the second division, there will be four nuclei in the basidium, and in the simplest case, these four nuclei ascend to the sterigmata which by this time have been formed, and the sterigmata bulge out at their apices where the unicellular spore is formed. This completes the life cycle of a "normal" representative of the Agaricales.

This life cycle can, consequently, be expressed by the following scheme:

### **1. Bipolar species:**

Basidiospore + → primary mycelium + → } dicaryotic mycelium → Carpophore →  
 Basidiospore - → primary mycelium - → }

→ binucleate basidiole → Basidium       $\begin{matrix} \textcircled{1} \\ \textcircled{2} \\ \textcircled{3} \\ \textcircled{4} \end{matrix} \right\}$  four basidiospores.

2.\* *Tetrapolar species* (Aa, Ab, Ba, ab, AB: pairs of Mendelian factors):

Basidiospore Ab → primary mycelium Ab → } dicaryotic mycelium → carpophore Ab.  
 Basidiospore Ba → primary mycelium Ba → } Ba →

→ Binucleate basidiole Ab. Ba – Basidium { o { o basidiospore AB or AB or Ab  
o { o basidiospore ab or ab or Ba  
o { o basidiospore Ab or BA or Ab  
o { o basidiospore Ba or ab or Ba

For taxonomic purposes, only the aberrations from this scheme are of interest, and as far as they present constant features, they can be used.

While diploid phases, common in Endomycetes, are rare and exceptional in Basidiomycetes (e.g. in *Coprinus*), there is a thus far unique life cycle type in *Armillariella* studied by Korhonen (*Karstenia* 20: 26, 1980) in *A. ostoyae*. In this species diploid pure cultures produce fruit bodies with clampless basidia where no fusion of nuclei takes place. In nature however, *A. ostoyae* develops dicaryotic subhymenial cells with haploid nuclei and two nuclei fuse in the basidium. It is now believed that the microspecies of the *A. mellea* group which in nature form clampless basidia have the same simple diploid life cycle as the cultures of *A. ostoyae*.

In 1934, Chow stated that in certain *Coprinus* the mature spores are binucleate; in 1933 Kühner reported the spores of *Marasmius rotula* uninucleate. Later (1945) he

\*Sec. Quintanilha, A., *Le Problème de la Sexualité chez les Champignons*. - Bol. Soc. Brot. 8(11), 1933.

indicates that in the Amanitaceae, Bolbitiaceae, Cortinariaceae, Strophariaceae, and most Agaricaceae, the spores are binucleate at the moment of discharge and afterwards. This is explained by the fact that the third division of the nuclei after meiosis (comparable with the third division in the ascii of the Ascomycetes, resulting in eight uninucleate ascospores) usually takes place in the spores rather than in the sterigmata or basidia and must result in binucleate spores. In most Hygrophoraceae and most Tricholomataceae, however, the third division takes place in the sterigma and only one nucleus ascends to the spore while the other descends back to the basidium where it degenerates. Thus, only one nucleus is present in the spore at discharge and immediately afterwards; however, the author has found this single nucleus dividing later on while still in the spore, and consequently some of the spores are then found to be binucleate and some uninucleate. The number of nuclei in the spore is easy to establish, and has undoubtedly great taxonomic importance. A new light has been thrown on this situation by a recent investigation by Duncan & Galbraith (1972) in which it was shown that not in all species and genera with uninucleate spores does the post-meiotic third nuclear division take place in the sterigma; these authors restrict this pattern described by Kühner to *Mycena alcalina* (and obviously some closely related species, or all Mycenas), and distribute the other Agaricales among two additional patterns whereby the last ("Pattern D") closely corresponds to what Kühner had described for all the species with binucleate spores. However, among those species which in normal (4-spored, heterothallic) sexuality and developmental behavior form uninucleate spores, Duncan and Galbraith distinguish another type ("Pattern C") in which the third nuclear division takes place not in the sterigmata but in the spore while it is still attached to the basidium, and the daughter nuclei distal to the basidium remain in the spore (one nucleus per basidiospore) while the other nucleus migrates back into the basidium. This pattern is characteristic not only for a number of white-spored Agaricales such as *Hygrocybe nigrescens* (Hygrophoraceae), *Hygrophoropsis aurantiaca* (Paxillaceae); *Polyporus brumalis* (Polyporaceae) and a majority of Tricholomataceae but likewise apparently all Russulaceae and all, even the brown- and dark-spored boletoid families including Gomphidiaceae (*Chroogomphus rutilus*), Paxillaceae (*Paxillus involutus*), Boletaceae (*Boletus*, 12 species).

In "pattern A", the third nuclear division takes place in the basidium; one of the resultant eight nuclei migrates into each basidiospore; if there are nuclei in excess of the number of basidiospores, they remain in the basidium and degenerate.

This pattern is characteristic for *Cantharellus*. It might have been possible to say that this pattern does not occur in the Agaricales were it not for a report on *Gerlonema setipes* (as "*Mycena swartzii* (Fr. ex Fr.) A.H. Smith") where both patterns A (*Cantharellus*-pattern) and C occur concurrently in the same carpophore. Since the carpophores studied by Duncan & Galbraith contained some bisporous basidia, the "dual pattern" of this species requires additional research. Generally speaking, there is a lamentably small number of species - and these all European - known enough in this regard to draw a conclusion to what degree the results are taxonomically valuable. Thus far, we can only conclude that exclusive existence in a carpophore with tetrasporous (or up to octosporous) basidia of "pattern A" is not

characteristic for any Agaricales and that we have here an additional character to separate the Cantharellaceae from the Agaricales. Furthermore it is remarkable that large groups (groups of families) are homogeneous as far as the post-meiotic nuclear behavior is concerned so that there is hope that while waiting for more complete data, a certain degree of generalization may be permissible. This, however, should be done with caution in the Tricholomataceae where apparently a minority exhibiting "pattern B", "pattern D" (*Flammulina velutipes*, *Oudemansiella*) and dual patterns exists with a majority exhibiting "pattern C".

In bi- and tetrapolar forms, the germ-tube and the whole initial stage of the mycelium is usually multinucleate and later becomes septate and uninucleate until copulation, whether it starts from a binucleate or a uninucleate spore. It is known, however, that in many cases, the mycelium resulting from germination of the spores is immediately binucleate, i.e. the uninucleate phase is not at all represented, and the life cycle of these species starts out with the dicaryotic mycelium. These forms are homothallic (Blakeslee 1904) and the thallus does not show any change of generations. Homothallism is obviously characteristic of the genus in *Clitopilus* (Kühner & Vandendries 1937). Many species are known in which homothallism is either the rule, or is found in special races of the main "normal" form. The latter case is frequent in such groups where 2-spored forms and 4-spored forms are known in a species (such as *Mycena*, *Mycenella*, *Galerina*, *Conocybe*, etc.) whereby the 4-spored form usually represents the normal form, and the bisporous form the homothallic form. Clamp connections are sometimes absent in homothallic forms but, of course, not necessarily so.

The life cycle of homothallic dicaryophytes can be shortly described as follows:

1. *Bisporous form:*

Binucleate basidiospore — dicaryotic mycelium — dicaryotic carpophore — binucleate  
basidiole — basidium  $\left. \begin{matrix} o \\ o \end{matrix} \right\}$  two binucleate basidiospores.  
 $\left. \begin{matrix} o \\ o \end{matrix} \right\}$

2. *Tetrasporous form:*

Binucleate basidiospore — dicaryotic mycelium — dicaryotic carpophore — binucleate  
basidiole — basidium  $\left. \begin{matrix} o \\ o \end{matrix} \right\}$   
 $\left. \begin{matrix} o \\ o \end{matrix} \right\}$  four binucleate basidiospores.  
 $\left. \begin{matrix} o \\ o \end{matrix} \right\}$

In other forms, the primary mycelium is able to form carpophores without previously forming a dicaryotic mycelium, i.e. every single spore (as in the homothallic-dicaryotic forms) is apt, theoretically, to form carpophores and another generation of spores without interference of another mycelium. In spite of the fact that these carpophores are necessarily composed of uninucleate hyphal cells, and there is no reduction in the basidium, the formality of the formation of uninucleate basidioles

is nevertheless conserved. The single basidial nucleus divides as in any other cell, and the resulting two nuclei move into the spores, one into each of the two spores. This is the case, for example, in *Mycena galericulata* forma *bispora*, and the fructification is then called parthenogenetic. Parthenogenetic carpophores, naturally, never have clamp connections. Even if the absence of clamp connections in the carpophore and the presence of but one nucleus in the hyphae can be demonstrated, the specimen is not a priori parthenogenetic, for one of the following reasons: (1) it may be that the sole nucleus is diploid whereby the fusion takes place immediately after copulation of the hyphae which may have been overlooked or without any copulation (and then the species would be homothallic-diploid). This situation is exceptional and perhaps restricted to *Armillariella* in the Agaricales although it has been shown that certain strains of Basidiomycetes form a permanently diploid mycelium (e.gr. *Coprinus lagopus*, *Schizophyllum commune*), and the diploid nuclei cannot be assumed to be confined to the basidia (cf. Casselton, L.A., *Genet. Res. Cambr.* 6: 190-208. 1965; Parag, Y. & B. Nachman, *Heredity* 21(1): 151-154. 1966); such diploid mycelia in *Schizophyllum* are, according to Parag & Nachman, constantly characterized by the presence, at each septum, of a pseudoclamp. - (2) It may also be that the sole nucleus is haploid until, by now unknown means, the basidioles become binucleate yet the four spores are again uninucleate. Here we have a life cycle in which the dicaryotic phase is shortened to the limit. Yet, this type of sexuality, the *Typhula*-type, has been observed in Agaricales only once (Chow 1934 in *Coprinus fimetarius*), and it remains to be shown whether this observation is correct, and if so, how common it is under normal conditions of culture and in the field. This shows that theoretically at least, in all cases, a complete cytological study is needed in order to arrive at exact results.

Morton Lange (*Dansk Bot. Ark.* 14: 1-164. 1952) has corroborated an observation by Sass (*Amer. J. Bot.* 16: 663-700. 1929) which refers to the fact that in *Coprinus sassii* (called bisporous form of *C. ephemerus* by Sass) both homothallic and heterothallic mycelia were raised from spores of the same carpophore. This behavior is intermediate between the fully heterothallic and the fully homothallic type as defined above, and the term amphithallism was introduced for it by Morton Lange. Amphithallic species and strains are not restricted to the genus *Coprinus* (where several species are now known to belong to it), but occur likewise in other genera, including in families other than the Coprinaceae, for example in *Conocybe pubescens* (Gillet) Kühn., *Agrocybe semiorbicularis* (Bull. ex St. Amans) Fayod ex auct. (2-spored race cf. *A. pediades*?), *Marasmius limosus* Quél. (bisporous!), *Galerina badipes* (Fr.) Kühn. f. *bispora* and *Mycena amygdalina* (Pers.) Sing. (bisporous!), all according to D. Lamoure 1960), also *Mycena rubromarginata* (Fr.) Kummer and *Clitocybe litua* (Fr.) Métrod according to Kühner & Yen (1949) and Kühner (1953), and a strophariaceous species determined as *Stropharia umbonatascens* Peck by Terra (1955). While it is true that in most cases of amphithallism, we deal with two-spored forms which form clamp connections, there are also a few uncontested cases of tetrasporous amphithallic species such as *Coprinus plagiopus* Romagnesi.

The parthenogenetic forms are, as far as we know, not characteristic for larger

taxonomic groups but merely for certain hereditary races, with "normal" and sometimes dicaryotic-homothallic parallel races. Consequently, the number of sterigmata on the basidia is not necessarily the expression of a certain type of life cycle, i.e. it is impossible to say whether it belongs to a dicaryotic-homothallic or a parthenogenetic form unless the nuclear divisions are carefully studied from the basidiole to the spore. It is probable, and, in the author's opinion, logical to expect that some of the normal (bipolar or tetrapolar) forms have died out, and the bisporous homothallic-dicaryotic, amphithallic, or parthenogenetic form alone has survived. Such seems to be the case, according to all taxonomic evidence, in certain species of *Laccaria*, and, perhaps being amphithallic, these species posses bisporous basidia as a specific character. As an example of bisporous "parthenogenetic" (basidioles monocaryotic) species *Omphalina rustica* (sensu Bresadola) should be mentioned; in contrast to this, the bisporous-monocaryotic form of *Mycena galericulata* is apparently conspecific with a "normal" (but rarer) tetrasporous form. Though, on the basis of the data available, it must be assumed that these bisporous *Laccariae* and *Omphalinae* as well as others actually are species\* this represents the exception rather than the rule, and we can now say that Lange (1914) overestimated the importance of the number of the sterigmata. Besides, the situation is not always as clear-cut as it may appear on a scheme. In many specimens with basidia developing sterigmata of a number lower than 4, the 2-spored basidia are intermixed with 1-, 3-, and 4-spored basidia\*\* which usually results in a marked polymorphism of the spores which vary between widely separated extremes of length and breadth, the volume of spores from 1-, 2-, and 3-spored basidia decreasing (in this order), and the 4-spored basidia developing the smallest spores. These facts can be explained by cytological irregularities - very frequent in fungi - which do not interest us here since their taxonomic value is close to nil. The significance of a concurrent development of 2-spored and 4-spored basidia should also be judged by the fact that young material may show more bisporous basidia than fully mature one, or vice versa and dermatobasidia may be more frequently bisporous than hymenial ones. The latter observation is frequently made in Boletaceae but has been confirmed in *Pleurotus* (Hilber 1982).

The complete absence of clamp connections can also by no means be linked with parthenogenesis exclusively. Clamps are often absent on the septa of binucleate hyphae, and there are rare, thus far not fully explained cases where clamps have been observed on the haploid mycelium. For taxonomic purposes, we may neglect the latter case, but if the presence or absence of clamp connections is used as a character in taxonomy, it is essential to make sure that the specimen studied is not

\*Morton Lange (l.c. 1952) also shows that in a number of cases, two-spored *Coprinini* should be considered as species, for example, in the section *Hemerobii* subsection *Setulosi*, the species *C. bisporus* Lange and *C. sassii* M. Lange & A.H. Smith, the former homothallic, the latter amphithallic, should be considered as independent. Indeed, M. Lange was able to show that between these bisporous strains and the most closely related tetra-sporous species, there are differences - although minor, but quite constant - of a morphological and cultural order.

\*\*In some Crepidoti, the four-spored basidia are thereby in a minority and this situation appears to be characteristic for some species or varieties of this genus and, curiously, linked with the abundance of pseudoparaphysoid cystidioles (Singer 1973).

merely a parthenogenetic form of a normally bipolar or tetrapolar species. If this possibility is excluded, we have further to deal only with species with normal sexuality that have lost their ability to form clamp connections, and homothallic forms, species, or genera, that find themselves in the same condition. Under these circumstances, the presence and absence of clamp connections must be accepted as a valuable character. Vendendries was the first to emphasize that a defined species has constantly clamps or is constantly clampless (i.e. in the non-parthenogenetic form). This statement is, as we shall see later, somewhat too exclusive but it foreshadows the use of the clamp connections in systematics. As a taxonomic character, they were first used by Singer (1942) and Kühner (in a foot note on *Tricholoma* in 1937, and again in 1945).

The presence or absence of clamps is a very good and usually constant character that can be used for units as large as families (for example Gomphidiaceae, Bondarzewiaceae, Russulaceae with exception of *Lactarius quercuum* which has clamp connections in the base of the stipe tissue), - all three characterized by the absence of clamps; Polyporaceae (with the exception of *Lentinus sulcatus*), Strophariaceae - both characterized by the presence of clamp connections), and for many genera (*Melanoleuca*, *Phaeodepas*, and many others without; *Laccaria*, *Tricholomopsis*, and many others with clamp connections) and groups of genera (most Lyophylleae, subfamily Panaeoloideae). In other cases, the presence or absence of clamp connections is characteristic only for subgenera or sections, or for minor stirpes, or it is merely a specific character. In only very few species, the clamp connections are completely inconstant as well as scarce, or they are confined to a certain definite position. Here, as in all characters, even the most useful ones, one can easily see that their value varies according to the group with which one is working. It often appears that the observer is not patient enough to search for clamp connections, or not experienced enough to search for them in the right place. If there are clamp connections, even in small numbers, anywhere in the carpophore but between hyphal cells exclusively (not at the base of the basidia), we may state that clamp connections are present. In *Armillariella*, whenever clamp connections have been observed, they are confined to the base of the basidia and sometimes to a few septa of the cheilocystidia or the covering layers. Only in the genus *Entoloma* there appears to be a necessity to define sections and/or species by the percentage of clamp connections found among the large number of hyphal septa and septa at the base of the basidia counted, and whether or not the base of the basidia is clamped (Kühner & Romagnesi 1953; Largent & Benedict 1971). Otherwise, the best place for the search for clamps is a layer consisting of filamentous, thin, thin-walled, not too densely interwoven hyphae; these are found, depending on the species, either in one of the covering layers - more commonly on the surface of the stipe than on the pileus, or in the basal tomentum, or in the hymenophoral trama, or in the tissue of the veil. A certain flexibility in the methods of the observer will be very advantageous. It should also be made a rule that a negative statement (clamp connections absent) should not be made unless several specimens from different locations have been patiently searched for clamps, and all septa observed have been found to be clampless. Doubtful (because of the early stage of the clamp formation or because

of optical conditions) clamps should not be taken into consideration. The clamps are either well developed at some septa, or not at all\*.

It is important to keep in mind that occasionally the clamps are formed in one tissue and not in another. This is especially true for densely interwoven layers consisting of thick-walled hyphae, and in intricately agglutinated tissues of cortical layers. Here formation of clamps may be actually suppressed rather than difficult to observe. The opposite can be observed in some species of *Galerina* where the hyphae of the connective "tissue" are found to be clampless while the fundamental hyphae have clamp connections. In *Pseudoclitocybe cyathiformis*, the mycelium has been observed to have numerous clamp connections, yet the carpophores are so constantly devoid of clamp connections, that this feature is used as one of the best characters for the distinction of this species. The opposite case (clamps present in carpophore - absent in mycelium) has also been observed in Basidiomycetes. It may well be assumed that those species with inconstant clamp formation as well as those where clamp formation has been abandoned except for a specific organ, can be considered as being in the evolutionary process of losing the clamp connections as an unnecessary and uneconomical\*\* way of cell division. It is therefore by no means surprising to find the transient species always in groups that, also according to the sum of their other characters, are intermediate between constantly clamped forms and completely clampless forms.

A further use of cytological characters derives from the fact that not all carpophores of the dicaryophyte have actually all single hyphal cells (i.e. the spaces delimited by wall and septa) binucleate. Hirmer, Brunswick and Kühner have shown that many hyphae and cystidia, especially the hyphae of the interior of the stipe, and the cystidia of such species as *Coprinus disseminatus* often contain more than two nuclei, i.e. they are actually coenobial cells where the septum between the single dicaryons has failed to form. The number of the nuclei, in such cells, varies from 3 to 54. Kühner (1945) attributes considerable taxonomic importance to these multi-nucleate hyphae and cystidia, at least he uses it in phylogenetic arguments. Counting of the nuclei in these cells has not yet become a routine of the systematist but this may not always be so.

The so-called *Godfrinia*-basidium, characterized by its development from a uni-nucleate basidiole, by the nuclear division taking place in the middle of the basidium (the basidium therefore attenuate above from a ventricose middle portion), and by the number of the sterigmata being two instead of four, with two uninucleate spores resulting, is not as marked a type as had initially (Maire 1901) been suspected. It is merely the basidium of a parthenogenetic haploid of the genus *Hygrocybe*. The genus *Godfrinia* based on it by Maire has been abandoned by all mycologists.

\*In the Aphyllophorales, a special type of clamps has been observed for many years which is remarkable for the space between the main hypha and the hook connecting the hyphal cells; this type of clamp is called medallion clamp. Medallion clamps are also quite frequently observed in Agaricales and Gasteromycetes but do not seem to have appreciable taxonomic importance (see Pl. 58, 2 ep) according to our present experience.

\*\*It is only fair to state that some cytophysiologists hold the opposite opinion.

Another basidium-type, the *Lyophyllum*-basidium, has, in contrast with the *Godfrinia*-basidium, great taxonomic importance. It is characterized by the fact that - everything else being normal - the nuclei are not readily seen because of a dense granulation inside the basidia if aceto-carmine is used for staining. This kind of content is called siderophilous granulation (formerly called carminophilous granulation). *Lyophyllum*-basidia, i.e. basidia with siderophilous granulation, are found in all species of *Termitomycetaceae* and *Lyophylleae* and (*Tricholomataceae*) and in some other families. A fragment of a not too young hymenophore is heated on a slide and kept moving in the medium which is the ordinary acetocarmine as used in cytological laboratories. When the first drop begins to evaporate and a film is beginning to form, the fragment is removed onto another slide; this is repeated twice, and the preparation is finally cooled off abruptly by putting the slide on a cold metal plate (microscope table); for stirring the fluid and for moving the fragment, a microscope needle is used whereby enough iron is dissolved by the concentrated acetic acid of the acetocarmine to deepen the coloration of the contents of the basidia sufficiently, as far as the siderophilous granulation is concerned. This granulation is then blackish purple to violet-black and rather dense. The method results either in distinctly granular basidia or in non-granular basidia; intermediate cases are not known. This method has the advantage of being applicable not only on fresh material but on well-dried herbarium material.

However, it is not unimportant that there are different types of siderophilous granulation. The Macro-type, most common in *Lyophylleae* and *Termitomycetaceae*, shows relatively very large particles (Pl. 9) whereas Micro- and Crypto-type are found in *Melanoleuca*, *Russulaceae* and in the *Entolomataceae*. *Russulaceae* and *Melanoleuca* show particles so small they are barely or not visible in the light microscope. In the so-called Oligo-type only a few well developed granules can be found, mostly in the lower portion of the basidium, and even these may be missing in many mature basidia. This type is characteristic for the genus *Hypsizygus*. The contents of the cystidia (and some basidia) of the genus *Tylopilus* are at first finely granular and inconspicuous but the granules later become large and striking. The basidia have been interpreted as another type of siderophilous granulation - the Giga-type - by Clémenton (1978); the cystidia as pseudocystidia by Wolfe and Singer.

While it is Kühner (1937) who has discovered this important character as a tool for the taxonomist, we have to thank Clémenton for his important contributions towards a refined technique, a better understanding of the cytochemical development of the *Lyophyllum*-basidium and electron-microscopic studies on the granulation. For details we refer to his papers (see bibliography) between 1968 and 1978.

Still another aberration from the normal can be observed in some basidioles that remain sterile. The fusion and the divisions in those bodies do not take place in the ordinary manner; their contents are visibly non-protoplasmatic (hence their "empty" appearance), and at maturity, instead of forming spores, these bodies become slightly larger or otherwise insignificantly different in size or shape from the normal basidioles. These bodies are called pseudoparaphyses (Pl. 22, 2). Their presence or absence, number, and distribution in the hymenium or on the edge of the hymenophore have a certain importance in systematics. But I find it, both in

theory and in practice, at times difficult to differentiate between pseudoparaphyses and cystidioles. In general, it may be said that cystidioles are more differentiated from the basidium and basidiole and that they occur principally in aequihymeniferous carpophores.

The indications given above show that many cytological characters as such are either useless or of thus far unknown use for the purpose of the systematist. At the same time, some characters that are closely connected with the study of the life cycle, sexuality, etc., yet not direct indications of any particular type of reproduction but rather "by-products" of the investigations on the latter, turn out to be of invaluable importance in taxonomy. The characters that are a direct expression of the sexuality of the Agaricales have not been studied in large enough number to allow any definite conclusions. It is not impossible (according to some data by Quintanilha and others, 1941) that the future will give the two categories of spore polarity the standing of a character in specific or even generic taxonomy, but in the only genera where extensive studies have been made, viz. *Mycena* and *Coprinus* (the former genus was investigated by A.H. Smith 1934, and Kühner 1938, the latter is since 1918 the favorite genus for sexuality research in Basidiomycetes because of easy culture methods and a wide variety of different behavior), the n-polarity of the spores, homothallism, parthenogenesis, etc. did not show more than intraspecific constancy, and seem to be due to minor (reversible?) physiological mutations.

On the other hand, minor details of the main types of life cycles, prove to be of enormous taxonomic interest, e.gr. the location of the third division (sterigma or spore); the presence or absence of clamp connections in cases where they have no or little connection with the sexuality of the species; number of the nuclei in the voluminous coenobial hyphae and cystidia that cytologically function as merely another part of the dicaryotic system; presence of a granulation in the basidia that is colored by the same dye that colors the nuclei, incomplete or aberrant divisions in the basidiole leading to the formation of pseudoparaphyses.

As for techniques of cytological investigations in the Agaricales, we cannot go into detail. However, it is recommended to start with an organism which is easy to collect in all stages, easy to fix and dye and uncomplicated in its development. Such a species is, for example, *Collybia dryophila*. It is advantageous to carry the fixative on collecting trips and insert the fragments, properly labeled, right in the field. Every genus, and every tissue, the mycelium, the basidium, and the spores, require an individual treatment as far as fixation and coloration are concerned, and there is no never-failing method that works with all cells of all fungi. However, Kühner (1938, 1945) has published repeatedly on the subject, and the chapter on cytology in his *Mycena*-monograph as well as a later article on the study of the distribution of the nuclei in the mycelia of the Basidiomycetes is recommended. Here, (as well as in R. Sandor, *Zeitschr. f. Pilzk.* 25: 103-108. 1959) good simplified techniques are described which can often be used successfully.

Techniques for monospore cultures and dicaryotization experiments for the study of the sexuality and compatibility of strains should be looked up in the respective literature of which we have cited only the most important contributions. Further

discussions would go beyond the framework of the present book, but significant facts will be mentioned in the Special Part.

Electron microscopy on the sterigmatal level has thus far not revealed much that might be considered helpful in Agaricales taxonomy or phylogeny.

The discovery of the "hilar appendix body" in both *Chalciporus rubinellus* and *Coprinus cinereus* by Yoon & McLaughlin (*Amer. J. Bot.* 66: 870-873) and illustrated in fig. 1-8 p. 871 l.c. is undoubtedly an interesting item but the far-reaching phylogenetical conclusions seem to be premature not only because of the differences observed in the formation of that body in the two species investigated, as pointed out by the authors themselves, but mainly because of the lack of data on other Agaricales, Gasteromycetes, and Aphyllophorales.

### *Pigmentation of the cells*

As an appendix rather than as an integral part of cytology, we shall now investigate another character that has to do with the anatomy of the interior of the cell and with cell physiology, i.e. the types and distribution of the pigments.

The rich and varied pigmentation of the Agaricales which surpasses by far that of the flowering plants implies the presence, in that group, of a large number of pigments, differing in regard to their chemical and physical particularities as well as their distribution on or in the hyphal (sporal, basidial, cystidial) wall or in the cell sap. Kühner has made a special study (1934) of the topography of the colored substances (as he expresses himself in the title) of the agarics and boletes. We shall here reproduce, in the outline, his classification of the pigments, and indicate examples for each type and subtype:

#### I. Intracellular pigments.

##### a. Present in the living cell.

1. Localized in the cytoplasma. .... *Cytoplasmatic pigments.*  
(*Leucocoprinus birnbaumii* - yellow globules; *Inocybe geophylla* - uniform).
2. Vacuolar. .... *Vacuolar pigment.*  
(*Amanita muscaria*, *Bolbitius* [yellow species], *Leccinum aurantiacum*, *Pluteus* spp., cf. Pl. 71, 2 ep), *Hydropus*.

- b. Appearing after death of the cell ("necropigment" according to M. Locquin 1953).  
(*Callistosporium*, all species).

#### II. Membrana-pigment\*.

(Elements of the cuticle of *Panaeolus sphinctrinus*).

#### III. Intercellular pigment.

(*Naematoloma fasciculare*; *Lactarius griseus* and related species; *Paxillus involutus*\*\*, *Suillus granulatus*; Pl. 27, 5).

\*We prefer now the term "intraparietal" for reasons indicated in Singer & Cléménçon (1972).

\*\*Atrotomentine, a 2,5-di-para-oxy-phenyl-3,6-di-oxybenzochinone has been analyzed and later synthesized by Kögl. It is the intercellular pigment of *Paxillus atrotomentosus*.

In a special chapter Kühner shows that the topography of the pigments in the Agaricales has taxonomic value. It has become a more important factor in systematics, since the number of single data, now accumulated (since Kühner's advice to taxonomists to describe the pigments observed) has grown considerably. In many families, species and higher taxa can be most clearly distinguished by the type and location of the pigment. Naturally, in many cases, two or more different types of pigments are combined either in the interior of the cells, or in the wall, or intercellularly. For instance, the reaction with  $H_2SO_4$  observed on the spores of certain Coprinaceae, and indicated above under "microchemical reactions", shows that there are two different kinds of pigment in these spores, one soluble and one insoluble in sulphuric acid. The same is true with pigment combinations in the cuticle of certain *Russulae* (*Russula*-red and *Russula*-yellow often combined\*). There may also be combinations of vacuolar and intraparietal pigment, and vacuolar and intercellular pigment, and intraparietal- and intercellular pigment (e.gr. in the boletes). It is often difficult to decide whether a pigment is intraparietal or intercellular-incrusting ("epimembranal"). It is a feature of the intercellular pigment to be easily dissolved (either after decoloration, or with a change of color when dissolving, or without any color change) in alcohol, ammonium hydroxide, even in water. Only few "epimembranal" pigments are insoluble in these solvents, and these are readily recognizable as superficial (e.gr. the resinous matter responsible for the colored crust on top of the colorless wall of the cystidia in some boletes). On the other hand, the true intraparietal pigments even though they have the appearance of "epimembranal" pigments because of the lack of elasticity of the outermost, darkest layer of the wall which then breaks off into fragments (spiral or areolate ornamentations), are always insoluble except in such brutal solvents as concentrated sulphuric acid.

Locquin (1953) adds special terms for pigments appearing by oxidation after bruising ("epipigment"), and those localized in the laticifers ("lacteopigment") and oleiferous hyphae ("oleopigment"), etc.

### *Oidial homing*

This interesting approach is most useful for infrageneric taxonomy. It has been treated recently by Kemp (in Clémenton, *Bibl. Myc.* 61: 259-276. 1977). For our purposes, it is of interest that Kemp observed lethal homing reactions between *Coprinus disseminatus* and other species of *Coprinus*, section (subsection) *Setulosi* which he interprets by concluding that "it would seem that this species is correctly placed in the genus *Coprinus*".

\*On pigment studies of *Russulae* see also p. 111, and Gluchov in Arpin & Fasson in Petersen (1971).

## XXII. PLANT GEOGRAPHY AND ECOLOGY

Plant geography and ecology of the fungi, and especially the Agaricales are so enormous in their theoretical and practical significance, so wide and ramified in spite of the superficiality of most of the data available, they can not really be treated here. However, the influence of data of this order on problems of taxonomy is too obvious to be ignored. There are all shades of opinions on the question whether or not the Agaricales have definite areas determined by the climate and its changes in history of plant life as admitted for Cormophyta. It shall not be denied here that the average geographic area of a representative of the Agaricales may be larger than the average area of an angiospermous plant. (It should likewise not be denied that the average area of an angiosperm is larger than that of an insect). But we have, in the Agaricales, everything from pantropical species and pantropical genera to endemics on tiny islands; we have typical vicariants, geographic races (which we call subspecies) that are fully the same as the geographic races of the phanerogams. The larger spores of the European *Suillus granulatus* showed it to be the type subspecies of a "circle of races" that was determined not merely by geography but also by mycorrhizal relationship: The American form was connected with 5-needle pines, and the European one with 2-needle pines.

Here we have a characteristic correlation between the fungus-host-relationship and the climatic factor. A form that differs from the other only in the host, not in geography, is called a mycoecotype (Singer 1940), provided minor morphological differences are also present. Otherwise, the distinction is based on experimental transplantation exclusively which would not be conclusive for Agaricales as much as it is for Uredinales (where the mycoecotype without morphological differentiation is known as ecological form).

It is quite obvious that the host-relationship, often taking the form of mycorrhiza partnership\*, is an important taxonomic factor since it often caused a regional if not geographic separation of the races involved and an independent evolution of both ramifications of the system in many cases. There is evidently a basic difference between the *Gymnopili* on frondose trees, on Monocotyledones, and on conifers. There is also a significant difference between the primitive *Russulae* and *Lactarii* that are non-mycorrhizal or forming tropical cicatrizer mycorrhiza and the higher forms that are mycorrhizal and even specialized. The *Sphagnum*-Galerinas appear to form definite taxonomical groups, and the constancy with which the *Suilloideae* confine themselves to mycorrhiza with conifers is undoubtedly no less impressive than the near-unanimity with which the *Leccina* favor the Fagales and Salicales. No less striking as a constant conifer-mycorrhiza, is the entire family Gomphidiaceae. Other ecological groups distinguish themselves by a prominence of forms preferring open places (outside the woods), gardens, greenhouses, lawns (e.gr. most of the Bolbitiaceae, which, even where entering the woods, never were found to form mycorrhiza). It is undeniable that all these ecological groups are at the same time

\*See also Singer R. & J.H. Morello. Ectotrophic tree mycorrhiza and forest communities. *Ecology* 41: 549-551, 1960.

taxonomic groups. Consequently, we feel safe to cite geographic and ecologic differences and similarities as auxiliary characters, supplementing and sometimes explaining the morphological and chemical characters.

It is too early to be very precise about the geographic areas and the ecologic characteristics of all the groups. The data available are, though by no means too scattered, yet, unfortunately, too unreliable. A citation of an agaric or bolete, without study of the specimen, by anybody less than a first rate specialist, is not a scientific document of any weight. Reducing our material by elimination of the doubtful, we finally arrive at a point where the material begins to become so scarce that, in some cases, conclusions can no more be drawn, and even in the remaining cases this can be done only in the three or four best herbaria of the world.

Under these circumstances, speculative theories, area maps, and conclusions reaching far beyond the available evidence have often been published. An improvement on the taxonomic methods, more collections, and less reliance on literature sources will eventually show that the agarics and boletes are an excellent field for those who are interested in the mycological aspect of historical plant geography and the evolution of the species in fungi. Only the richness of a large herbarium, with a few genera worked out according to the standards of modern taxonomy, will circumscribe clear areas, and even these will be corrected by further planned collecting in the border regions.

But even now, it can be seen that certain genera or groups of species have a characteristic distribution or ecological requirements. Thus, a large number of genera is obviously of intertropical distribution (*Pseudofavolus*, *Mycobonia*, *Arthrosorella*, *Asproinocybe*, *Podabrella*, *Termitomyces*, *Pleurocollybia*, *Aphyllotus*, *Phaeodepas*, *Agaricochaete*, *Physocystidium*, *Chaetocalathus*, *Amyloflagellula*, *Palaeocephala*, *Manuripia*, *Epicnaphus*, *Hymenogloea*, *Pegleromyces*, *Filoboletus*, *Pleuromycenula*, *Mycoalvimiia*, *Pseudohiatula*, *Callistodermatium*, *Clarkeinda*, *Volvolepiota*, *Micropsalliota*, *Janauaria*, *Smithiomycetes*, *Hiatalopsis*, *Horakia*, *Ripartitella*, *Melanotus*, *Pyrrhoglossum*, *Neopaxillus*, *Phyllobolites*, *Phlebopus*, *Phylloboletellus*), only occasionally venturing into the warm-temperate zone of both hemispheres. Others are obviously restricted to parts of Asia (*Psiloboletinus*, *Lampteromyces*) or the south-temperate zone (*Crucispora*, *Cuphocybe*) while innumerable taxa are strictly north-temperate. The Gomphidiaceae have their natural area, as a family, within the area of the Pinaceae, and *Melanomphalia* as well as *Descolea* have large areas all their own, without entering the long list of clearly cosmopolitan genera such as *Galerina*. The distinction of *Omphalina* from *Gerronema* is aided by the fact that the basic pigment-characters are paralleled by a difference in ecology and phytogeography since most species lacking yellow, pink, and carotenoid pigments in *Gerronema* are strictly tropical-subtropical whereas *Omphalina* with its incrusting dark pigments is restricted to boreal, temperate and tropical-alpine habitats. *Ripartites* differs from *Neopaxillus*, aside from morphological and chemical characters in the fact that the first, with one exception contains only temperate species, whereas *Neopaxillus* is tropical and subtropical exclusively. Moser was struck by the fact that the ex-subgenus of *Cortinarius*,

*Dermocybe*, was very scantily represented in the rich Patagonian Cortinariaceae-flora which added to the morphological and chemotaxonomical evidence in favor of separating it as an autonomous genus. The list of examples could be greatly enlarged if infrageneric taxa were included in the discussion. Phytogeography, if its data are well founded on extensive herbaria-studies and monographic work, can also contribute very interesting and valuable data for the historical plant geography of certain regions as has been shown by an analysis of the antarctic fungus flora (Singer & Corte 1962; Singer in Antarctic Map folio series 5, 1967) and the interesting studies by Malloch, Pirozynski & Raven (*Nat. Acad. Sc. USA.* 77: 2113-2118. 1980) and Pirozynski (*Austr. Journ. Bot. Suppl. Ser.* 10: 137-159. 1983).

### XXIII.

## PHYLOGENETIC THEORIES CONCERNING THE ORIGIN OF THE AGARICALES

The phylogeny of the Agaricales is still a controversial field. The history of phylogenetic systematics of the Agaricales has been analyzed at length in a previous paper by the author\*. It is intended to give, in the present chapter, an account of the arguments used and the views expressed in accordance with the facts now available. The accumulation of facts, found in a search for supporting data for one's own hypothesis, or for the purpose of invalidating an opposing argumentation, would in itself be justification enough for the serious discussion of this subject - a subject that seems to be so utterly "theoretical" for some scientists. It is generally acknowledged that only paleobotany can ultimately prove the direction of progress and regression, yet all the other available data taken together often give a rather convincing picture of the evolutionary trends in certain groups, and only those who refuse to recognize it because of prejudice against evolutionary theories in general, will deny the high degree of probability in certain parts of the phylogenetic schemes proposed.

Among the facts brought to light in comparatively recent times, we have to mention the connection existing between certain Gastromycetes on one hand and certain Agaricales on the other hand, and between certain Agaricales on one hand and certain Aphyllophorales on the other hand. It will be enough to study the whole series of forms between the extreme "Astrogastraceae" and the extreme Russulaceae as has been done by Buchholz (1902), Lohwag (1924), Malençon (1931), Heim (1938), Singer (1936-1939, 1962-1963), and Singer & Smith (1959-1960), or the series from *Galeropsis* to Bolbitiaceae-Strophariaceae (Singer 1939, 1951, 1955; Heim 1950), or from *Truncocolumella* and *Gastroboletus* to *Xerocomus*, *Boletus* and *Boletinus* (Malençon 1938; Zeller 1939; Singer 1942-1945; Singer & Smith 1959), or from *Brauniella* to *Volvariella* (Singer 1953), or *Thaxterogaster* to *Cortinarius* (Singer 1951; Singer & Smith 1959), or from *Montagnea* to the Coprinaceae in order to lose all illusion about the sharpness of some of the key-characters allegedly distinguishing the Gastromycetes from the Agaricales.

\*Das System der Agaricales. *Ann. Mycol.* 34: 287-310, 1936.

On the other hand, real or apparent transitions from the Aphyllophorales to the Agaricales were suggested in large number in order to satisfy the hypotheses - dominant for many years - of derivation of the Agaricales from the Aphyllophorales. The collapse of all the speculation about a relationship between the Boletaceae and the Polyporaceae, based by Neuhoff & Ziegenspeck on a *Gyrodon* with allegedly white spores, and by others on Henning's *Filoboletus*, is complete. The *Gyrodon* turns out to be *Boletus edulis*, and its spores are not white but - absent, and *Filoboletus* turns out to be a pore-bearing form of the marasmoid Tricholomataceae. A careful revision of the tramal structure of all Boletaceae (Singer 1945) has established the fact that all boletes have more or less bilateral hymenophoral trama, a structure unknown in the Polyporaceae (except *Panus prancei*) and polyporoid Aphyllophorales. White spore print also does not exist in the Boletaceae, and the genus *Leucogyroporus* was based on an erroneous observation by Murrill, while *Polyporoletus* Snell turned out to be a *Scutiger*.

However, other connections between the Aphyllophorales and the Agaricales have been uncovered recently. The author does not enter the argument about an alleged affinity between *Cantharellus* and *Hygrophorus*. It may be enough to say that a collective group, an assemblage of notoriously unrelated species, such as Fries's genus *Cantharellus*, can be used to prove the affinity with numerous other groups, exactly as many as there are represented in the collective genus in the first place. While there are elements of *Clitocybe*, *Hygrophoropsis*, *Leptoglossum*, *Geopetalum*, *Cantharellus*, *Gomphus*, to name only a few - there is, as far as is known to the author, no representative of the Hygrophoraceae hidden in *Cantharellus*. Should it have been the bright yellow-orange or red color of some *Cantharelli* and some *Hygrophori* that first suggested the affinity?

As it turns out now - with modern pigment-chemical data at hand - a bridge can indeed be seen in the pigmentation of certain species of *Cantharellus* on one hand and - not the Hygrophoraceae - but *Gerronema* on the other hand, and the hypothesis might be advanced that *Cantharellus*, at least *pro parte*, can be derived from *Gerronema* or vice versa, as long as the cytological differences are ignored.

There is likewise a definite affinity between *Polyporus* sensu stricto and allied polypore genera on one hand, and the Lentineae (lamellate Polyporaceae) on the other. As we shall see in the chapter on the Polyporaceae (p. 163-190), this affinity is indeed demonstrable and undeniable. However, I have seen the solution in a simple transfer of the Lentineae to the Polyporaceae sensu stricto. The question is now whether there is, as has been assumed earlier, a strong hiatus between the Polyporaceae sensu stricto and the aphyllophoraceous polypores such as Scutigeraceae, the Coriolaceae, and the poroid Thelephoraceae. Prominent mycologists like Donk thought that the hiatus between the aphyllophoraceous polypores and the Polyporaceae sensu stricto is small, and does not justify a separation of the polypores in the wider sense into agaricoid and aphyllophoraceous polypores, or at least that such a separation was at that time not feasible. While the present author is deeply convinced that such a separation is not only feasible but necessary, it must be

assumed that the acceptation of Donk's point of view lends itself to the hypothesis that there is a "bridge" between Aphyllophorales and Agaricales by way of Lentineae-Polyporeae-Coriolaceae, and possibly Scutigeraceae.

In a study of the types of the so-called *Laschia*-complex, Singer (1945) attempted to draw a line between the "true" Agaricales (*Dictyopanus*, *Filoboletus*, and especially *Poromycena* = *Mycena*) and the other laschioid Basidiomycetes (excluding the original *Laschia* which belongs to the Auriculariaceae) which were considered as belonging in the suborder Cyphellineae in a wide sense. It was also said in the same paper, that certain Tricholomataceae with always lamellate hymenophore, such as *Panellus*, *Hohenbuehelia*, *Resupinatus* might conceivably be close to a group deriving from these cyphellaceous genera rather than from any Gastromycetes. Since it now appears that the Cyphellineae themselves are a rather artificially mixed group (Donk, Singer), they have lost their phylogenetic importance as a starting point, and *Favolaschia* becomes solely allied to a part of *Aleurodiscus* unless more facts supporting the connection between *Favolaschia* and *Dictyopanus* become available in order to make the bridge between *Favolaschia* and the Agaricales something more than speculative\*. By the same token, *Campanella* and *Leptoglossum* can now be shown to be related not so much to each other or to the Favolaschias or Cantharellaceae respectively as to some agarics, in the case of *Campanella* - *Marasmiellus*, and in the case of *Leptoglossum* - *Omphalina*.

A further "bridge" between Aphyllophorales and Agaricales might be seen in *Linderomyces*. This genus has been shown to be very closely related to *Gomphus* (Petersen 1971), indeed, Petersen goes so far as to identify *Linderomyces* with *Gloeocantharellus*. I believe that my insertion of *Linderomyces* in the Paxillaceae (1947) was a mistake but it is obviously an understandable conclusion that because of the existence of *Linderomyces* the limits between the Agaricales and the Aphyllophorales are also narrowed down at the level of Paxillaceae vs. Gomphaceae. It was formerly thought that bilateral hymenophore is strictly an agaricaceous (Agaricales) feature. If, because of *Linderomyces*, this attitude has to be abandoned, the temptation is great to conclude that in a group with often weakened or indistinct bilaterality like the Paxillaceae, there is a tendency to develop into an aphyllophoraceous (Aphyllophorales) group with the same instability of hymenophoral structure, or vice versa, that the latter is a starting point for an evolution which would lead from the Gomphaceae to the Paxillaceae. There is only one complicating fact: that such an evolutionary trend would, by necessity involve clavarioid and resupinate forms.

All these affinities, assumed or otherwise, make the question timely again, that has been asked before: What exactly are the limits between the Agaricales and the neighboring orders of Basidiomycetes? It has come to the point where the answer to this question cannot be given by an agaricologist alone but becomes a problem that must seriously concern those working on Aphyllophorales and Gastromycetes.

\*As for the affinities of *Favolaschia* (Favolaschiaceae) see Singer, Monograph of Favolaschia, *Beih. Nov. Hedwigia* 50, 1974.

There are those who doubt that there is a gap inside of what was formerly considered a solid group - the Aphyllophorales.

There are those who doubt that there is a gap in what is usually considered - if not a natural group - a strongly convergent group of strictly parallel lines, the Gastromycetes.

If both are right, i.e. if there are no gaps in either case, and the three groups intergrade with each other without so much as an appreciable hiatus there are only three alternatives for the phylogeny of the Agaricales:

1. The Agaricales are interpreted as an intermediate group between the Aphyllophorales and the Gastromycetes, with the Aphyllophorales the starting point, and the Gastromycetes the summit.
2. The Agaricales are an intermediate group between the Gastromycetes and the Aphyllophorales, whereby the former are considered as the starting point ( or points), and the latter as the "summit".\*
3. The Agaricales are a genuinely polyphyletic group with one part derived from the Aphyllophorales, the other from the Gastromycetes.

The hypotheses (1) and (2) have the disadvantage of suggesting that the evolution supposed to have taken place, runs in an immense circle. In fact, starting as we do, from the assumption that no convincing dividing lines between Agaricales, Aphyllophorales, and Gastromycetes exist, we have to admit that the only reasonable derivation of the Gastromycetes as a whole is that outlined in rare concordance by nearly all specialists of the Gastromycetes, i.e. an evolution starting at a low point of the Basidiomycete-system, and running parallel with the Tuberales of the Ascomycetes, finally reaching the most highly developed, unipilous forms of the Phallineae and the agaric-like Secotiaceae, Hymenogastrineae, etc. If, then, no gap is allowed between the Agaricales which would be derived from the Gastromycetes and the Aphyllophorales, the latter would become merely strongly reduced agarics, step by step sinking backwards and downwards to the level where the Gastromycetes were supposed to have started. The same (vicious) cycle results if the direction is reversed.

All three alternatives have been advocated. Alternative (1) is practically identical with the position taken by Savile (1955). Alternative (2) is practically identical with a theory tentatively advanced by Kreisel (1969). Alternative (3) is the only one which expresses the various phylogenetical hypotheses proposed by A.H. Smith since 1959.

This is the place to discuss the probabilities of Savile's scheme. Savile is no doubt a very competent mycologist whose phylogenetical theories about the origin of the rusts have to be respected as presenting a defendable theory - not shared by the present author - but as far as the Agaricales, Aphyllophorales, and Gastromycetes are concerned, Savile feels (p. 111) that "a detailed attempt to trace the evolution of

\*In spite of the fact that Kreisel later changed his opinion, we shall in the following pages refer to this phylogenetic view as Kreisel's hypothesis (Kreisel 1968).

the Higher Basidiomycetes is beyond the scope of this paper and the qualifications of the author". Without a detailed knowledge of the Higher Basidiomycetes, it is, however, impossible to go on to "consider the factors that seem to have controlled evolution in the Hymenomycetes". These factors are in Savile's scheme and phylogenetic trees basically erroneously interpreted and therefore lead to erroneous conclusions. In the first place, palaeontological data (Dennis 1969) have clearly demonstrated the fallacy of Savile's fundamental postulate that the clamp connections are not a primitive but a derived characteristic of the Higher Basidiomycetes (see also Singer 1970, p. 77), and his second postulate considering the true parasites as the ascendants of the whole of the saprophytic (and mycorrhizal) Higher fungi is at least debatable. Both postulates are clearly in contradiction with the views indicated by most leading mycologists of our time. This is not to say that some parasitic or otherwise strongly specialized forms may not have preserved, in certain cases, primitive characteristics which may be indicative of evolutionary trends of the past. The sentence (p. 92) "The 'Hymenomycetes' evidently arose from a group of parasitic Auriculariaceae just after the origin of the clamp connections but before it became a constant feature" is therefore not acceptable, and the basic reasoning which leads to further discussion of the derivation of Clavariaceae and Gasteromycetes as well as Agaricales is consequently invalid. But even the discussion of the status of these "higher" groups contains so many unfounded statements and leads to so untenable conclusions that it is necessary to review them here in some detail.

If indeed bridges from the Aphyllophorales (as enumerated above) do exist, they would all lead from physiologically and/or morphologically highly organized organisms to lower organized ones. *Cantharellus* is ectotrophically mycorrhizal - *Gerronema* is saprophytic; Favolaschiaceae are anatomically highly organized saprophytes which by loss of some of their high organization would, by way of the Panellae, lead to mycenoid genera where a highly developed obligatory parasitism (as in *Mycena citricolor*) occurs; saprophytic corticioid genera would lead by way of clavarioid ones with symbiotic features to pileate ones with mostly saprophytic nutrition, following an evolutionary line from *Ramiricium* to Paxillaceae whereby the clavarioid genus or genera would appear as a link between resupinate and pileate carpophore configuration, quite in contrast to the terminal position Savile attempts to concede to the clavarioid fungi (p. 94-97). As for the Gasteromycetes, Savile claims (he is not the first to do so) that "the opposite view [to that expressed by him, i.e. derivation of Gasteromycetes from the Agaricales] would entail the independent development of the typical forcible discharge mechanism of the Basidiomycetes in each of the evolutionary lines that connect the two groups". The typical forcible discharge mechanism is a highly successful mechanism which is obviously the only viable spore discharge mechanism to which the apobasidium can evolve, and if there were several avenues of evolving towards the typical autobasidium it cannot be seen why - in favor of endocarpism - it should have been abandoned at several points of the Agaricales independently without leading to a more favorable and more economical way of dispersal, and lead, always, to the same simple type of holobasidium. The rain-drop-splash-model refers only to one highly developed and strongly derived group, Nidulariineae, rather than any more primitive group of the

Gasteromycetes, and the dispersal of hypogeous fungi by rodents (cf. Savile p. 96, and Singer 1958, p. 30) is far from general since many Gasteromycetes are dispersed by insects, ants, worms etc. and the more primitive ones may be (and apparently are) entirely independent of rodent dispersal. This is, even if it were correct, only a partial argument since many of the Gasteromycetes which are close to the Agaricales, in fact the majority, are epigeous.

What apparently bothers Savile and his followers is the fact that from several evolutionary lines which lead from the "polyphyletic" Gasteromycetes to the "polyphyletic" Agaricales - in my view, neither of these orders is polyphyletic - would end up in the same type of basidium-spore-configuration characteristic for the "hymenomycetous" autobasidium. This objection, however, is completely futile for two reasons. First of all, because the transition from apo- to autobasidium in the Gasteromycete-Agaricales-complex does not, in reality, lead to one single type of discharge mechanism and a single type of basidium-spore-configuration. Singer & Grinling (1967) have already shown that there are different types of autobasidium (see p. 41 and 72), and more different types will eventually be found inasmuch as the basidium in its auto-holo-form is by no means uniform. Secondly, and this is more important, there is no reason at all to assume that the autobasidium has been formed during development in several parallel evolutionary lines. Nobody is - or should be - naive enough to suppose that a bridge between Gasteromycetes and Agaricales has been historically functioning by following a chain or series of recent genera with the characteristics derived from the study of recent species. All such sequences of ever-more (or ever-less) agaricoid Gasteromycetes are supposed to show is that a general evolution in one or another direction has taken place, in some cases, step by step, and that such a step-by-step development does point in a certain direction, but the "real", "historical" development may very well, and must even, have taken a parallel, similar course. Thus in the case of the evolution from Gasteromycetes to Agaricales, or vice versa, if one prefers, the ancestors of our recent families of Agaricales may have had, and very likely have had an autobasidial structure and biology. This is probable because of the fact that already on the level of *Hydnangium* a development of autobasidia with exposure of the mature hymenium has taken place which leads to *Laccaria*. It will be objected that by accepting this kind of reasoning, we come to the result that apparently very different spore types - which have now been taken as serving for the differentiation of different "orders" in the Gasteromycetes, are actually found, side by side, in closely related branches of the Gasteromycete system. I am firmly convinced that this is so, because there is much more spore type variability in the Gasteromycete families than there is in the Agaricales families. And there is also a great deal more basidial variation in Gasteromycetes than in the Agaricales (sticho- and chiasto-basidia, subisodiametric and strongly elongated basidia, hymeniformly organized basidia and fascicled bunches of basidia, Tulostoma-basidia and acro-sporulating basidia, sterigmata with asymmetrically attached spores, and sterigmata with symmetrically attached spores, and even phragmo- and holobasidia if one includes heterobasidial endocarpic fungi). It may well be admitted that "it is to be expected that [the discharge mechanism] would quickly be suppressed in any species that

became angiocarpic" (Savile, p. 96), but wherever we can observe "gasteromycetation" as in *Lentinus*, *Panus*, the "gastroid form" of *Suillus decipiens*, or the gastroid mutation of *Psilocybe*, the endocarpic carpophoroids etc., this expectation does not come through. Quite on the contrary, the trend towards endocarp, where it exists at all, is triggered by a deficiency in some such necessary factor for normal development towards gymnocarp as light. It has been argued that the tendency towards hypogeous development may lead to lack of light and therefore to endocarpic development, but one fails to see what could have triggered a trend towards angio- or endocarp in a *Psilocybe* supposedly developing towards and into such groups as the Weraroas which are neither hypogeous nor, for that matter, xerophytic, but hygrophytic and strictly epigeous. The widely held but erroneous opinion which attributes to all obviously agaric-like Gasteromycetes like *Hybogaster*, *Weraroa*, *Galeropsis*, *Panaeolopsis*, *Endolepiotula*, *Gastrocybe* to name only a few, either hypogeous development or adaptation to xerophytism, should by now have disappeared from the arguments of phylogenetic speculation.

Savile also - without factual evidence - repeats the statements of older mycologists and of Heim that the veil of the agarics and boletes is not functionless. It should by now be obvious that there are many kinds of "veil", of very different origins, and that the veil as such cannot be taken as a fore-runner of the outer peridial layer, nor can it be taken as a protective organ in the mature carpophore. There is no successful branch in the Agaricales where the double veil is more than the characteristic of the more primitive members of a family; it invariably tends to be reduced wherever an evolutionary line develops towards successful modern branching-out as can be seen in the Russulaceae, the Coprinaceae, the Agaricaceae, the Amanitaceae, the Paxillaceae, the Pluteaceae.

The specialized dispersal systems invoked by Savile for the purpose of giving evidence to the idea that the Gastromycetes (as a whole) are a derived and polyphyletic group, are not at all convincing inasmuch as the Agaricales show similar and additional dispersal systems. The highly developed entomochorous dispersal system found in some Phallineae is obviously meaningless in this argument since nobody since Brefeld has claimed that the Phallineae are ancestral to the Agaricales.

While one cannot but whole-heartedly agree with Savile's basic principle that "new major groups are never derived from climax groups of the parental stock but always from unspecialized lower groups of great genetic plasticity", one finds oneself confronted with Savile's postulate that the new major group of Gasteromycetes as a whole is derived from what is evidently a climax group like Russulaceae, the Strophariaceae, or *Cortinarius* (the largest genus of Agaricales known!).

All these objections make it unavoidable to reject Savile's scheme as distorted by insufficient familiarity with the facts as far as they refer to the higher Basidiomycetes, and by inner contradictions between his arguments and his basic principles. These objections will not apply to the opposite theory, proposed by Kreisel and the various hypotheses advanced by A.H. Smith and collaborators. Although I personally believe that a reduction from the Agaricales to the "lowest" Aphyllophorales is, to a certain degree, too simplified a view on the whole of Basidio-

mycete evolution; while I also believe that the assumption of a trend towards angiocarp or endocarp in some families of the same complex where a trend from endocarp towards gymnocarp is admitted, is somewhat unlikely and unsatisfactory, both alternatives (2) and (3) cannot be rejected out of hand.

To these alternatives we may add those derived from an assumption that there is indeed a gap or hiatus of considerable magnitude inside the Aphyllophorales, (before the agaricoid polypores have been eliminated from the Aphyllophorales and the so-called agarics with Aphyllophorales-affinities like *Lentinellus* from the Agaricales) - or else that there is indeed a gap or hiatus of considerable depth between the Agaricales and their obviously related counterparts in the Hymenogastrineae and "secotiaceous fungi" on one hand, and the rest of the Gasteromycetes (the true Gasteromycetes or Plectohymeniales of Malençon and Heim).

This leaves, as viable and defendable theories, (a) the alternative (2) and (3) and (b) the two possibilities outlined in the preceding paragraph. Since it cannot be the task of the present discussion to decide on the origin of the Aphyllophorales or on the origin of the ("true") Gasteromycetes, but merely to discuss the sensible alternatives regarding the origin of the Agaricales, we may combine Kreisel's ideas with those advanced by the present author, and confront them with the ideas of Heim and his school, leaving open the contention advanced by Smith who, in a way, admits the possibility that both the derivation of the Agaricales from Gastromycetes, and of Gastromycetes from Agaricales can co-exist.

Consequently, the three logically possible and actually important theories of today, each of them defended or favored by a group of systematists, are the following:

- I. Derivation of the Agaricales from Gastromycetes.
- II. Derivation of some Gastromycetes ("Exogastrineae") from some Agaricales, and the Agaricales from certain Aphyllophorales.
- III. Derivation of some Gastromycetes from the Agaricales, and of some Agaricales from the Gastromycetes.

It cannot be stated at present that the probability of one of these theories is overwhelming enough to fully refute the others. A taxonomist with enough practical experience and theoretical background can only give one a slight edge over the others, expressing a preference. In spite of the author's preference for theory I, the attempt will be made to state the case for each of them.

#### *A. Derivation of the Agaricales from the Gastromycetes*

This theory has been defended in detail by Singer (since 1936) after a number of authors, ever more explicitly, had voiced similar ideas (Brefeld 1876; Buchholtz 1902; Lohwag 1924; Dodge 1931; Singer 1932).

In all fungi, fructification is originally achieved without intercalation of a specialized fruiting body (carpophore) between the mycelial (vegetative) thallus and

the sexual sporulation stage. In all major groupings of the Eumycetes, carpophores are first (i.e. in the most primitive, least differentiated forms) endocarpic, viz. with internal sporulation. In the Zygomycetes, the only kind of carpophore known is endocarpic (*Endogone*). In the Ascomycetes, we may take the plectomycetic series as the first one to develop carpophores and these are closed (cleistothecia or perithecia). Even in the primitive Discomycetes the beginning of carpophore formation is characterized by hemiangiocarpous development or (*Ascodesmis*) by ascii developing from a basal (hyphal) layer and surrounded by filamentous, sterile "paraphyses" which also originate in the basal layer. In other probably primitive groups, like Telebolaceae, Elaphomycetaceae, Sordariaceae, as well as in the fossil *Palaeosclerotium* (see also discussion on p. 145) the carpophore is likewise endocarpic. It is true that a majority of mycologists follows Malençon in deriving the Tuberales from the Discomycetes and it has been even suggested that this evolutive tendency should be paralleled by the Gastromycetes which, then, would be derived from the "Hymenomycetes". But this theory is not convincing and the actual direction of evolution in these Higher Ascomycetes may much better be read inversely whereby an inverse tendency, in Discomycetes, comparable to gasteromycetation may or may not be involved. In the Endomycetes (in the sense of Kreisel), the only carpophores ever formed are characterized by endogenous sporulation. Whether we recognize these lower asco- and basidiomycetes as a class or not, it cannot be doubted that they have primitive characteristics. In the Basidiomycetes, I consider it as indicative that the development of *Hoehnelomyces delectans* (Auriculariales) shows (Möller 1895) at first a primordium of interwoven hyphae which develop a coremium-like stalk consisting of erect parallel hyphae. In the further course of development an apical head is formed consisting of hyphal ends which will eventually become basidia. This head will soon become covered by hyphal ends derived from a calyx-like outer spreading tissue of the apex of the stalk just below the head and will recurve over the head to form a loose tissue of hair-like hyphal ends. This peridium-like organ is formed much earlier and becomes denser, gelatinized, and rather thick in *H. javanicus* (Weese 1919). The earliest fruiting body, in its earliest stage, the coremium-like stalk is fertile in culture (with basidia) but in nature it is sterile and ends up in a gastrocarp. Quite in contrast to Savile's ideas on the origin of the clavarioid carpophores, a beginning of clavarioid stalks leads up to endocarpic sporulation in these primitive organisms because this is the only type of fructification which, in nature, benefits by a protective covering. This is easily understandable because, in contrast to the hymenia protected by a superimposed pileus or gastrocarp or because it develops on the lower side of the substratum, it is here exposed to rain and evaporation without having an apparatus which guarantees rapid spore expulsion as we have in the Discomycetes, where the young stages are covered by an epithecioid layer. As a matter of fact the role of the paraphyses in the Discomycetes is apparently taken over by the "paraphysis-like" - as they are described - hyphal ends of the head-covering of *Hoehnelomyces*. The description of the development of *Hemigaster* by Juel (1895) corresponds to the development of *Hoehnelomyces* in many ways, and is an example of early carpophore production in the Homobasidiomycetes. In both cases we have a pseudoendocarpic and stipitocarpic development. The gleba is at first undifferentiated, but in

the Protogastraceae we have a beginning of tramal plates and this may lead to more highly differentiated carpophores. The co-existence of pigmented and hyaline spores in the Phleogenaceae shows that the spore characters in the early Gastromycete-like Basidiomycetes are still variable and fluid and will gradually adapt themselves to endocarpic sporulation by becoming more resistent. The difficulties in basidiospore dispersal in such primitive forms are compensated for by the abundant production of conidia.

It is therefore not surprising that some mycologists looked for endocarpic ancestors when they were searching for the origin of the "Hymenomycetes", whether this is seen as a single event or a tendency to be found in several lines of basidiomycete evolution. It was, consequently, important to find bridges between the two main groups representing endo- versus exogenous sporulation in the Higher Basidiomycetes, and it is the merit of Buchholtz, Lohwag, and particularly Malençon to have constructed such a "bridge" between the two groups. The first such bridge was that of the so-called astrogastraceous series. But this effort, whatever its factual merits and its interpretation, has entailed an ample research on often rare and "exotic" groups whereby finally modern methods of investigation - often borrowed from the modern research methods in Agaricales rather than Gasteromycetes - have been used and which have shown that, at least in some instances, data could be found which can give the direction of this evolutionary trend. Furthermore, this research has demonstrated that all major groups of Agaricales had links with Hymenogastrineae or "secoiaceous fungi", and that in certain cases one particular group of Gasteromycetes could be linked with two or several families of Agaricales. This latter observation, particularly striking in the case of *Hydnangium* which shows clear relations not only to the astrogastraceous series but also to Tricholomataceae (*Laccaria*) and Hygrophoraceae (*Hygroaster*) suggested that the direction of development was from *Hydnangium* towards the agarics rather than vice versa. Looking, then, for primitive characters in *Hydnangium* as compared with the rest of the astrogastraceous series including the Russulaceae, it was found that *Hydnangium*, as a generic character, shows clamp connections, considered, as we have seen (p. 128) correctly, as a primitive character in Basidiomycetes. We find that these are lost as we ascend towards the Russulaceae where the absence of clamp connections is (nearly) a family character.

Since the Russulaceae as true mushrooms develop a fleshy pileus out of the peridium and since the thickening of the pileus-trama originated at the expense of parts of the gleba, it is not unexpected that the spherocysts which are characteristic of the hymenophoral trama or parts of it in the asterogastraceous series, produced, perhaps under pressure, spherocyst nests in the trama wherever the hymenial surface was suppressed. It has been claimed that the spherocysts, in the fleshy Agaricales, merely serve the expansion by volumen and the coherence of the trama, but as much as this may be a by-product of the heteromerous structure in the Russulaceae, it is not at all the only way for large, fleshy agarics to construct a voluminous coherent trama. Similarly large, fleshy pilei are achieved in other groups by gelatinization of the tissues, by developing sclerotization of the hyphal walls or eventually di- or trimitic trama, or else by simply increasing the hyphae in a system of interwoven

elements, and finally by a gradual reduction of the trama or inflating of the filamentous hyphae into short, voluminous hyphal chains, as in *Mycena*.

The columella is originally a thin column of widened hymenophoral plaques and of the same anatomical structure as the latter. Widening into a stipe, it will most naturally also assume heteromerous structure like the pileus. The columella in *Macowanites* has already this structure.

This indeed is the only explanation of the extraordinary heteromerous structure in the Agaricales, and this fact is important because in this regard the Russulaceae are unique in the Agaricales. Any attempt to derive the Russulaceae from other "Hymenomycetes" must fail because of the absence of this structure in other families and even in such genera which may otherwise be considered similar - *Porpoloma*, *Melanoleuca*\*. If it were only a question of homoio- vs. heteromerous structure, it might still be possible to derive the Russulaceae from other Agaricales but it is well known that Russulaceae share with the Elasmomycetaceae-Hydnangiaceae also other characters, such as the cystidial characters and the latex, the specific ultrastructure of the spore walls and certain characteristic elements of the cortical layers, all of which are not shared with either *Porpoloma* (or for that matter with any Hygrophoraceae) or *Melanoleuca*. The difficulty of deriving the Russulaceae from any other group but the astrogastraceous series is an additional argument in favor of their derivation from gastromycetous fungi.

The development of a functional large stipe from which a pileus-like upper portion of peridium + gleba is being lifted whereby the lower portion of the gleba is exposed, leads to a situation where this upper fertile portion of the carpophore emerges sufficiently or is isolated from the humus or duff to expose the lower portion of the gleba making a free spore fall possible at least for the superficial portion of the hymenophore. Under these circumstances two developments - both realizable in the Gastromycetes - would show to be advantageous for the dispersal of the spores:

- (1) Transformation of all or part of the gleba into a hymenophoral configuration which permits free spore fall for all of the spores; this can be achieved by transformation of the tramal plates into lamellae or tubes. This transformation will be possible as soon as the tramal plates become geotropic. Gastromycetes, even without having become agarics, are, as we now know, fully capable of producing such a hymenophore (*Gastrocybe*, *Galeropsis*, *Panaeolopsis*, *Endolepiotula* etc.).
- (2) Once such a transformation of the trama has been achieved, the free fall of practically all spores will be possible if the spores, instead of gradually separating from the sterigma and adhering to the hymenium, were propelled a few hundred  $\mu\text{m}$  off the hymenial surface. This advantage according to our observations can be obtained - and the resulting organism will be more successful in competition, - by a transformation of the apobasidium of the Gastromycetes into an autobasidium characterized by an asymmetric spore attachment to the tip of the sterigma

\*This genus has the clampless hyphae and the Micro-type siderophilous granulation of the basidia and an amylaceous spore ornamentation like the Russulaceae; see also p. 107.

(spiculum), whereby the role of a water drop at the suprahilar region of the spore, whatever its biophysical role, seems to be of some significance. If this spore dispersal type is coordinated with a postponement of the sporulation period until all the hymenophore is exposed, it marks the point where the Gastromycetes become "Hymenomycetes" or, at any rate, Agaricales. From this point on, they are capable of producing a spore print. They have entered the tremendously successful group of Higher Basidiomycetes which show all kinds of variation of this type of basidium-sterigma-spore configuration and spore dispersal mechanisms. They are now evidently more competitive, as epigeous organisms, and therefore begin to form large groups of recent genera in full evolution. Their ancestors and related endocarpic organisms, on the other hand, remain in the position of rare, almost relictual, taxa, mostly with the characteristic island-like areas of distribution often shown by taxa in retreat, or else they have adapted to certain ecological conditions which are inaccessible to the hymenomycetous fungi such as hypogeous carpophore production, extreme xerophytic conditions, or else they have otherwise adapted to specific means of spore dispersal (Nidulariineae, Phallineae, Lycoperdineae). This then is the reason for the preponderance of hypogeous and xerophytic species in the groups of Gasteromycetes close to the Agaricales. It cannot be an adaptation to such habitats and subsequent loss of the autobasidium because by far not all Gasteromycetes closely allied to certain agarics are hypogeous or xerophytic.

The autobasidium thus achieved is not the product of a single mutation but rather, as has been suggested by Singer & Smith (1960), the final step in a series of evolutionary events based on predispositions. Thus, in Gastromycetes as far removed from the Agaricales as *Torrendia*, *Octavianina* and many of those that are closely allied with the agarics and boletes, there is a tendency to form sterigmata which are curved - these are often the ones that are not fully apical -, and such curved sterigmata often produce axially asymmetrical spores. How this predisposition of Gastromycetes-spores may in the end lead to a functional discharge apparatus has, as a working hypothesis, been explained in the paper quoted above.

If the recent, vigorously developing groups, such as the Russulaceae which in addition to everything else, have also acquired an ectomycorrhizal relationship and thus occupied the whole vast area of the ectotroph distribution, are considered as the starting point of a series of much less successful, saprophytic genera - which have lost their symbiotic relationship, we find ourselves in contradiction with the "age and area" rules and Savile's most basic principles. I have (1955) given a few figures (Table II, p. 23) on the number of species in genera of Agaricales compared with that of genera of related Gasteromycetes which show that the former are invariably much richer in species (some of the figures should now be changed since more species are known in both cases, but the relation remains always the same). It can be shown likewise that the area of the gasteromycete genera is considerably more restricted than that of the agarics and boletes close to the former.

The development of the carpophores of the Hydnangiaceae is not well enough known to make it part of an argument either in favor or against the theory here discussed. It has now become clear that the veil, in contrast to the typical volva, is

the product of interaction of the hyphae of hymenophore and/or pileus-margin, and/or stipe surface. Studies on the development of the primordium of *Hydnangium carneum* (Petri 1902) show that a gymnocarpic *Russula*-like primordium, by an early, strong incurvation of the lateral part of the "pileus" (gastrocarp) extends to the base of the "stipe" (columella), without, even after maturity, opening up to expose the gleba. I have (Singer 1958, p. 28) called this type pseudoendocarpic, regardless of whether a postmaturation exposure of the hymenophore is achieved, and do not think it can be called gymnocarpic since free spore fall and full exposure of the hymenium is not possible in these fungi because of the configuration of the gleba. If the incurving margin after interaction with the hyphae of the surface of the stipe and because of this interaction produces a veil which remains as an annulus, and the hymenophore is already lamellate, while the peridium has developed into a thin-fleshy pileus, we have obviously a primitive and early form of agaric. Therefore one is tempted to suppose that the Russulaceae section *Pelliculariae* are a primitive type of Russulaceae, a supposition which is confirmed by the fact that in this group a constant obligatory ectotrophic mycorrhiza is not yet general (my own observations in the neotropical forest), and that this group shows all the characteristics of the least derived representatives of *Russula*, including light colored to white spore print, subacute to acute margin, mild taste, little variation (few species) and sharp hiatus between species\*.

In the further evolution of the genus, we find that the veil is gradually reduced because it cannot and does not have a function favoring further adaptive development. Even in the most notorious annulate *Russula*, *R. annulata*, we have already an exannulate form. Veil-rests of other Russulaceae, viz. section *Subvelatae*, are already of such a consistency (silky-pulverulent) that it does not and cannot interfere with free spore fall, and even this is confined to only a few species. The successful, common, ectomycorrhizal higher Russulaceae do not show any veil and have passed from primary or secondary angiocarp to gymnocarpy.

We have elaborated on the probable direction of evolution in the case of those series that are leading from a natural and well studied group of Gasteromycetes, the Hydnangiaceae, to the Agaricales. Other lines of research have uncovered other bridges to the Agaricales, which shows that the connection with Agaricales and a strong affinity between some Gasteromycetes and most or all Agaricales is not restricted to the astrogastraceous series. These newer results have now become so rich in detail - monographs of many genera have been published with modern approaches to their study - so wide in scope (see table III) and so rich in undeniable facts that they have been unanimously accepted as proving the affinity between Gasteromycetes and Agaricales in general. None of these researches has uncovered facts that would suggest that in the other links between Gasteromycetes and Agaricales the opposite direction of evolution is more probable; some data would - on the contrary - suggest that the same direction of evolution is to be assumed (see also Singer 1958, Singer in Petersen 1971, Singer 1977). One will find it highly probable that in these series which involve the same transformations similar forces

\*Cf. Singer, Araujo & Ivory, *Beih. Nova Hedwigia* 77: 287. 1983.

have been at play and similar, with variations of sequence, directions of evolutionary tendencies should be assumed.

We must assume that the tendency of the gasteromycetoid apobasidium to produce resistant spores (with a thicker and often more complex spore wall structure) will disappear with the final transformation of the apo- to a physiologically functional autobasidium which makes a resistant and well isolating spore wall with postponed germination unnecessary and wasteful. Consequently, in Cortinariaceae, we have a gradual reduction of wall layers (Clemençon, see p. 85). Obviously, then, *Thaxterogaster* can hardly be considered an end-product of this line of evolution but must be close to its origin. Here, as in other cases (e.gr. *Gastroboletus*), the macro-evolution leading from Gasteromycetes to Agaricales is obscured by the fact that a probably much more recent phenomenon - gasteromycetation - can be observed in agaric or bolete genera.

I have to repeat here what I first stated in 1958, that it is by no means claimed that any of the families or other taxa of Agaricales proved to be related to certain genera of Gastromycetes are direct descendants of these gastromycete genera as we now know them. It is possible and perhaps probable that the actual ramification leading to the lines that eventually are traceable to the various families of Agaricales has taken place at the moment when a common ancestor of the recent hymenogastraceous genera started its transition from apo- to autobasidium. This would contribute to a better understanding of the difficulty of presenting the families of Agaricales in a logical sequence of mutually most-related families or of constructing an expressive phylogenetic tree. In a linear system, the families of Agaricales cannot be placed in a fully satisfactory manner and it might be best to visualize the origin of the Agaricales in the manner of ascending rays, which at a certain plane representing the recent Agaricales flora, are clustered into groups which represent families. According to a numerical assessment of their characters, some of these families are closer to one than another but they are not - unless they have a common ancestral line forking immediately below the recent level, such as maybe in the complex Polyporaceae, Hygrophoraceae, Tricholomataceae or Amanitaceae-Pluteaceae - phylogenetically related one to another in the sense that on the agaric-bolete level, they have arisen one from another or all of them from aphylophoraceous ancestors. Only in this sense can we call them monophyletic. Certainly, in our view they are not polyphyletic in the sense that they derive from unrelated ancestral stock.

Thus, the problem boils down to the question whether the suborder Hymenogastrineae (to which, in my opinion, all those Gastromycetes belong which could possibly have given rise to the Agaricales) is a mono- or polyphyletic group, a group which - long before the transformation of the Agaricales into Gastromycetes or vice versa could have taken place - must have originated very early in the history of Basidiomycete evolution. That this has indeed been so, is corroborated by (1) the affinity of some of the agaric-like Hymenogastrineae and secoziaceous families with what Malençon (1955) has called "Endogastrineae" e.gr. *Torrendia*; (2) the concept of the classical school (Fischer, Zeller) that sees the Gastromycetes as a natural taxon and the Hymenogastraceae as a low, still plastic and malleable unit of this

Table III  
Affinities of Agaricales-families with Gasteromycetes and Aphylophorales

Hymenogastrineae	Secotiaceous Hymenogastrineae	Gastromycetation	Agaricales	Aphylophorales
		Lentodium-forms	Polyporaceae	
Maccagnia	Hydnangium		Hygrophoraceae	
	Hydnangium		Tricholomataceae (Laccaria)	?Cantharellaceae p.p.
?Torrendia	Brauniella		Amanitaceae	
			Pluteaceae	
Maccagnia	Endolepiota		Agaricaceae	
	Notholepiota			
	Endoptychum			
	Neosecotium			
	Secotium			
	Polyplodium ss. Sing.		Coprinaceae	
	Montagnea			
	Panaeolopsis			
	Gastrocybe		Bolbitiaceae	
	?Tympanella			
	?Tubariopsis			
	Nivatogastrum		Strophariaceae	
	Galeropsis*			
	Weraroa = Clavogaster			
Hymenogaster	Thaxterogaster	sect. Hemicortinarius	Cortinariaceae	
	Volvigerum			

Protoglossum	Setchellilogaster Cribbea ?Gigasperma		Crepidotaceae
Richoniella	Rhodogaster  Paxillogaster Singeromyces Gymnopaxillus Austrogaster Brauniellula		Entolomataceae  Paxillaceae  Gomphidiaceae
Rhizopogonaceae ?Le Ratia	Gastroboletus Truncocolumella	gastroid  Suilloideae	Boletaceae
Gautieria	Chamoniaxia		Boletaceae
Octavianina up to Hybogaster	Macowanites		Russulaceae Bondarzewiaceae ?Auriscalpiaceae

\*May at the same time be related to the Bolbitiaceae.

whole. The present fashion of speaking of the Gastromycetes as an assemblage of unrelated "orders" has so much become a part of "modern" systematics and phylogenetic thinking that it is difficult for mycologists to change this concept. Yet, the idea of dividing the gastromycetoid fungi into unrelated "orders" has had its origin in the application of modern methods of research taken from the Agaricales. The supposed differences of many of these orders (Russulales, Boletales, Hymenogastrales, etc.) merely project basic differences between Agaricales families into the Gastromycetes. And if one may think that these basic differences have arisen in the Agaricales (as for example the heteromerous trama structure), it should also be permitted to at least postulate that they have arisen in the Gastromycetes. Indeed, the spore characters are, in each gastromycetous family or "order" by far more variable than they are in the corresponding families of Agaricales, and, what is more important, they are less correlated with other characters than they are in the Agaricales. If we imagine a single character of the spore - its pigmentation - lost in *Chamoniaxia* it would go into another order (from "Boletales" to "Rhodophylales"); these examples could be multiplied. Indeed, if *Secotium* or *Endoptychum* had a still stronger tendency to pulverulent gleba than they have anyhow, they would be transferred to the "Lycoperdales".

Taking all this together, it is although not impossible but highly improbable, that there exists a gap deep enough to distinguish two orders - let alone classes - between the agaric-like Hymenogastrineae and secotioid fungi on one hand and the remaining Gasteromycetes on the other. The argument, then, that the former cannot have any other origin than the only one left - from the Agaricales - is not a strong one and can be dispensed with in the frame-work of the theory here explained.

### B. Derivation of the Agaricales from Aphyllophorales

The author has the task to revitalize a theory that was originally based on the faulty assumption of a bridge between *Polyporus* and *Boletus*, and another between *Cantharellus* and *Hygrophorus*. However, it seems that the same result will be obtained if more reasonable suggestions are followed up. For example, one may assume that the line leading to the higher tropical polypores of the genus *Microporus* continues by the way of *Microporellus* Murr., and finally reaches into the genus *Polyporus* sensu stricto, whereby the turning of a poroid hymenophore into a lamellate hymenophore would be merely a repetition of an analogous development in the Coriolaceae. It may also be assumed that there might be a real relationship between the meruliaceous and meruliod genera *Plicatura*, *Rhodoarrenia*, on one hand and *Arrhenia* sensu stricto on the other. *Arrhenia* is close to *Leptoglossum* and *Omphalina*, the latter being possibly derived from the former. Finally, it may be assumed that *Favolaschia* is something like a halfway mark between the Corticiaceae and the Panelleae, and it may then be considered as possible that the direction of the evolution is from *Aleurodiscus* to the Tricholomataceae. These three potential bridges do not necessarily exclude each other; they may be parallel.

A fourth bridge may be seen by those who follow Romagnesi in recognizing aphyllophoraceous affinities in *Lentinellus* while at the same time conceding some sort of relationship with Polyporaceae or Tricholomataceae (Leucopaxilleae), or Russulaceae or Bondarzewiaceae, among the Agaricales.

A fifth bridge may be seen in the assumed relationship between the Paxillaceae and the Gomphaceae which has come to light through recent studies on *Linderomyces* by Singer, Petersen and Corner. Here all depends on whether *Linderomyces* was correctly placed in or near the Paxillaceae as proposed by me (1947). In the same spirit, one may also, in spite of the difficulties, (ectomycorrhiza and stichobasidia in *Cantharellus*) postulate an affinity between *Cantharellus* and *Gerronema*.

Corner (in several recent papers) has postulated an origin of boletoid genera, especially *Meiorganum* and *Gyrodon* from Coniophoraceae. Such an affinity - Kühner (1977) does not admit it - may be interpreted in different ways (both boletaceous and coniophoraceous genera derived from Gasteromycetes e.gr. *LeRatia*; both Rhizopogonaceae and Boletaceae derived from Coniophoraceae; Coniophoraceae derived from Boletaceae, etc.). The Boletaceae-Coniophoraceae - link is partly corroborated by pigment chemistry (see also under *Meiorganum* p. 746-748).

Agerer (1983: IMC 3, Abstracts p. 366) takes the possession of a subiculum in some cyphellaceous fungi as an indication of their origin from subiculum-bearing Corticiaceae from which he attempts to derive the Agaricales.

With the reservation that these bridges may or may not\* express real affinity and that the trend of the evolution might also be read (as would certainly be the case in Kreisel's hypothesis) as going in the opposite direction, we may assume that a derivation of the agarics from certain Aphyllophorales is still a viable proposition and that the gap between Aphyllophorales and Agaricales is not as deep as those believe who prefer the opposite hypothesis (see p. 125, 127). There is certainly a tendency in the Agaricales towards loss of the hymenophore as is evidenced by the reduced series (cyphellization) in three families of the Agaricales. But it may well be assumed that there is also a gradual trend towards a more elaborate hymenophore starting from smooth hymenial surface and veins (as in the Cantharellaceae and perhaps the Gomphaceae), running parallel with or anteceding the opposite trend. There is certainly, as stressed repeatedly by A.H. Smith, a tendency in Agaricales from pigmented spores and colored spore print towards less pigmentation (as evidenced in *Inocybe*) but other cortinariaceous spores of the fungi involved in the alleged bridges between Aphyllophorales and Agaricales may also show a tendency towards intensification of the pigmentation. There is indeed no other way of passing over from the genera mentioned above as possible links between the two orders to dark-spored groups like the Bolbitiaceae and Coprinaceae, Strophariaceae and Cortinariaceae. Furthermore, all the genera involved in this speculation being veillless, it would have to be assumed that the development of veiled forms, even volvate species and genera, is a consequence of increased differentiation - an assumption

\*The transfer (and thus establishment of a cross-connection between Agaricales and Thelephorineae) of the genus *Horakia* to the "Thelephorales", as proposed by Oberwinkler (*Sydowia* 28: 359-361. 1977), merely on the basis of spore shape, is not convincing.

which demands some proof (not yet available in general terms) of the usefulness of the veil at any stage beyond the primordium in any major group of Agaricales. But assuming that the veil is an organ which, at least in several groups of Agaricales, favors survival, it may well be argued that the original primitive evelate forms eventually tend to produce a veil or veils and volvas. Or it may be assumed that in the ontogenetic evolution of the Agaricales it was unavoidable that a number of them developed veils and volvas in a transitional stage, losing it eventually again. Indeed Reijnders' suggests (1963) that "angiocarp should be considered a useful adaptation during the development of the primordium". Lacking experimental proof for this postulate (for example comparing the development of primordia with angiocarpous development with the same primordium with removed covering in varying conditions such as humidity) and lacking an explanation for the usefulness of veils acquired by secondaryangiocarpic development, one may still consider Reijnders' and Heim's opinion as possibly correct.

By allowing all three assumptions to be tentatively accepted, one is faced with the problem of constructing a possible line of development towards the forms with well-formed lamellate or tubulose hymenophore with strongly pigmented spores and well developed veils and volvas. This problem can be solved if the origin of certain groups is considered as not (yet) satisfactorily explained. I have already mentioned the difficulties of derivation of the Russulaceae from any other Agaricales; the only promising possibilities might be discovered by searching for aphyllophoraceous ancestors of the Bondarzewiaceae (Hericaceae? Auriscalpiaceae?) since the Bondarzewiaceae are the only\* Agaricales-family with real affinities with Russulaceae (see p. 803-804). As for the rest of the families, one may construct a line leading from the Tricholomataceae to the Amanitaceae (by way of *Armillaria* and/or *Armillariella*, *Cryptotrama*, *Termitomyces*, etc.), from the Tricholomataceae (Lyophylleae, *Lepista*) to the Entolomataceae; from the Paxillaceae and/or Tricholomataceae to the Crepidotaceae; and from the Tricholomataceae to the Agaricaceae (by way of the Cystodermateae). From these derived families it would be relatively easy to pass over (trough the pale-spored forms) to the Strophariaceae and Cortinariaceae and perhaps from here or from the Agaricaceae to the Coprinaceae and Bolbitaceae. The boletes can be derived directly from some bolete-group ancestral to both them and the Paxillaceae, and the Gomphidiaceae may be part of a side line called "Phyllobolotales" by Heim (in Petersen 1971), which would be in agreement with A.H. Smith's (l.c.) ideas.

At a certain level of development in the Agaricales - in certain families like the Tricholomataceae and Paxillaceae at a still very low level - a tendency towards gastromycetation becomes visible. In some families, as in the Polyporaceae, this tendency would be confined to the phenomenon discussed in chapter VI as gastromycetation, while in others it would lead to a polyphyletic group of agaric- and

\*Theoretically, one may also see *Amanita* sect. *Roanokenses* (Amanitaceae) as a starting point of the Russulaceae because of the analogous origin of the spherocysts in the trama and the existence of ornamented, amyloid spores in *A. roanokensis*. However, the hiatus between the two families is so wide and the dissimilarities so conspicuous that it is not surprising to find that, as far as I am aware, not even those who postulate a derivation of *Russula* from other Agaricales have seriously discussed this possibility.

bolete-like "Exogastrineae" in which gastromycetation becomes irreversible because, we must assume, these forms have found an ecological niche which permits their survival. This survival is, according to Heim and his followers, guaranteed by the possibility of producing carpophores in the dark, hypogeaously, and under xerophytic conditions (where their endocarp might actually mean a certain advantage). These, in further morphological "degradation", might develop into moderately successful small families such as the Rhizopogonaceae and Hymenogastraceae, perhaps aided by a newly acquired ability of entering ectotrophic mycorrhiza as in the case of *Rhizopogon*. But these new niches would be blind alleys limited as they are, by the gap between Endo- and Exogastrineae, postulated by Heim and Malençon. Unlike A.H. Smith's scheme, Heim's general phylogeny would not permit them to re-acquire their lost autobasidial capacities and re-enter the system of Agaricales proper. If we reverse the arrows, we may illustrate the origin of Heim's Exogastrineae by our Table IV, or directly pass to Heim's (1971) Fig. 3 (p. 527).

This theory explains the origin of the families of hypogeous and perhaps xerophytic Exogastrineae. It fails to explain or make plausible the origin of the genera *Weraroa*, *Gastrocybe*, and all the other epigeous, hygrophilous species of the Exogastrineae. Admitting that it is not impossible to find ways to come to an ad hoc explanation of the adaptation of these forms to gastroid development, or to find some ecological or experimental way of making it plausible - which has not yet been done - we are here, to use Heim's expression "in the wide open field for hypotheses".

Resuming, it is possible to maintain a theory which postulates an aphyllophoraceous origin of the Agaricales and the origin of the "Exogastrineae" by degradative processes.

### C. Derivation of the Agaricales from both Gastromycetes and Aphyllophorales

If I interpret A.H. Smith's current thought on Basidiomycete phylogeny as expressed during the Hesler Symposium (Petersen 1971) correctly, he would assume that agarics have given rise to some families of Gastromycetes, for example *Laccaria* → *Hydnangium*; Gomphidiaceae → *Brauniellula* and that these gastromycetous groups show again a trend towards Agaricales, such as *Hydnangium* → Russulaceae. "Violent spore discharge only begins again when the fruiting body begins to open up", he says, and [the forcible spore discharge] "is not coming de novo because it was probably in the original ancestors. You have to think in terms of a circle" (p. 499, 500). Where would this view leave *Laccaria* and *Gomphidius*? Smith is not very explicit regarding the supposed origin of these genera. He merely says "that an overall correlation of characters can be shown, probably indicating relationship in the progression from the simple clavarioid fungi through *Clavariadelphus*, *Craterellus*-like fungi (with more or less smooth hymenium) and *Cantharellus* to *Hygrophorus* on one hand and *Clitocybe* on another". At any rate, it would appear that an aphyllophoraceous ancestry of some Agaricales is assumed,

and this would tend to leave the derivation of the Gomphidiaceae and probably the Cortinariaceae to be resolved in much the same way as has to be envisaged according to Heim's ideas or the way explained in the previous chapter (p. 148).

Since Smith does not elaborate much further, it is difficult to see how he would pass such hurdles as the chiastobasidium being transformed (in the Cantharellaceae) into a stichobasidium and then, in spite of the irreversibility rule, return to the chiastobasidium (*Hygrophorus*, *Clitocybe*); or, thinking in the way of circles, have the autobasidium (*Laccaria*) return to an apobasidium (*Hydnangium*) only to return afterwards to the autobasidium (Russulaceae) or vice versa. I do not claim that these hurdles are insurmountable, but thus far they exist and no solution has been offered. A solution, however, would be desirable since Smith is evidently attempting to limit his acceptance of the progressive evolution from Gastromycetes to Agaricales to those cases where the likelihood of such an evolution is best documented.

### Conclusion

I do not consider the problem of the origin of the Agaricales - or for that matter of the other orders of the Higher Basidiomycetes - solved, and I agree whole-heartedly with statements made by Petersen (1971) in the discussion of the problem when he says "When you say you have no connection to a certain taxon, this must be tempered by the possibility that the connection might be uncovered..." (A.H. Smith: "If someone finds intermediates then we can change the map").

This is valid not only for connecting links (which may have disappeared without leaving a fossil trace) but also for other aspects which might influence our thinking on Basidiomycetes evolution. The chemistry of the pigments is undoubtedly of primary importance in a group so extraordinarily rich in pigment variations as the Basidiomycetes. Kreisel (in Demoulin, Intern. Symp. Biol. Ges. D.D.R., p. 115, 1968) states that "taxonomical work with Gasteromycetes has something in common with Paleobotany. The fruiting bodies grow slowly and (exist) for a long time" which suggests the importance of studying the complete development of the key species and the importance of the longevity of the carpophores. Enzyme studies might also be helpful. But data on all these and other aspects are scarce and generalizations dangerous. This can be seen by the fact that mere rationalizing led R. Heim to state (in Petersen 1971) that hypogeous fungus carpophores and "angiocarpic" forms have spherocysts in the trama because "it is necessary for the angiocarpic form to swell in size underground and that the russulas and others are light because they are outside". The truth of the matter is that hypogeous carpophores have been found which are lighter in weight than any known epigaeous fungi (Smith mentioned his genus *Mycolevis*), and that there are Russulaceae and other Agaricales which have as heavy a specific weight as any Gastromycetes both fresh and dried (e.gr. *Boletus torosus*). All these lines of argument will become or might become valuable once we have a complete list of figures on such characters and precise studies on their ontogeny, always considering the ecological conditions under which a certain line of evolution is proceeding.

Under these conditions, I appreciate such measured and objective discussions of the matter as were given by Kühner (1948), by Demoulin (*Les Gasteromycètes*, p. 13-20. 1969) and others. And I am happy that Heim, the principal promoter of the degradationalist theory, has abandoned his rigid attitude stating that "Each (thesis) has its strengths, each its weaknesses. But if plausibilities carry most mycologists toward one theory rather than another, no certainty, no essential and sufficient peremptory indication underlies such a verdict" (Heim 1971).

It is generally assumed that lack of paleontological evidence must necessarily leave our final judgment in complete uncertainty forever. I am not convinced that this is so. In the first place, once more reliable and quantitative data are accumulated, and studies of the world flora more complete and more detailed, the arguments in favor of one single theory may become overwhelming enough to make it generally acceptable. In the second place, even if this were nothing but a fond hope, the scarcity of paleontological evidence is not a condition as everlasting as it may seem. A petrified basidiomycete from the middle cretaceous - already highly developed and *Fomes*-like (Singer & Archangelsky 1958), early carbonaceous saprophytic mycelia with typical clamp connections (Dennis 1969) and the prospect of palynological evidence shown by the fact that *Laccaria*-spores could be demonstrated without a doubt in profiles studied by Hernandez and Singer in Sphagneta of Southern Chile - are signs that possibilities do exist in this direction.

Still more important, material from the Middle Pennsylvanian originally described as *Palaeosclerotium pusillum* shows cleistothecia with ascospores, the latter in both shape and size as well as ornamentation extremely like those of the Cribbeaceae. At the same time, the hyphae have clamp connections and dolipores which suggests an early rise of paired nuclei (dicaryons) in a fossil Ascomycete. Having myself studied the original photos taken by Dennis (*Science* 192: 66-68 illustrated only part of the serial sections), I am satisfied that, contrary to suspicions voiced later, the clamped hyphae actually belong to the same individual fungus that produced the cleistothecium. The similarity of this species with *Cribbea* as pointed out by me (*Mycologia* 49: 850-854. 1977) is startling even though the carpophores of the Cribbeas are much larger than those of *Palaeosclerotium*. If indeed a secotioid fungus is closely related to a fossil Ascomycete, it becomes increasingly probable that the former are descendants of the Ascomycetes rather than the Agaricales. On the negative side, it becomes necessary to be careful with statements suggesting that the Basidiomycetes first appeared in the carboniferous since the clamped hyphae observed thus far may as well be those of an Ascomycete as of an early Basidiomycete.

#### XXIV. ON THE DEFINITION OF TAXA

##### The lower taxa

While the "Agaricales in modern taxonomy" is essentially a generic monograph, the enumeration of examples for each genus and its subdivisions brings up the

question of what is to be considered a species. Lacking evidence to the contrary, it has been assumed since Vandendries's basic work, that in the Agaricales the normal and typical species is not interfertile with other species. As for subspecies, this term is here used in the sense of Wettstein, for a race. In fungi, such races can also be distinguished not only in the sense of climatic-geographical races but of races connected with different host- and symbiont-adaptation wherever such a connection has become constant in nature and is accompanied by minor morphological or chemical differences. There are also examples for seasonal diploformism as studied by Wettstein in the phanerogams, for example the summer- and winter-fruiting races of some Suilli, likewise accompanied by minor morphological differences. Furthermore, we have the bisporous and tetrasporous races of certain agarics like *Mycena galericulata* for which, irrespective of the nature of bisporicity ("parthenogenetic" or homothallism), the term "forma" is now in general use when there is no other but sexuality differentiation. If there are also morphological differences, these are generally on the specific level. In other words, bisporous agarics may be independent species just as bisporous families and orders exist (Dacryomycetales). But the taxonomic situation of the bisporous forms of morphologically non-differentiated agarics is still open to discussion and further elaboration.

Where we have obviously infraspecific taxa about which important data (exact extension of area or host range, hereditary character of its diagnostic characteristic(s), the degree of intersterility, etc.) are unknown, the favored taxon is: variety. This is largely the same as Salisbury's (in Huxley 1940) "putative variety". Where no constancy or reduced interfertility is present, the use of "forma" is justified - as long as this has any taxonomical interest whatever.

I have (1943 and in Cléménçon 1977) discussed these matters more extensively and in more detail, giving examples and I do not find it necessary to repeat these here. I must, however, appeal to taxonomists in general and to monographers of fungus groups in particular, to define what their understanding of the taxa is. If an author chooses other definitions for good reasons, this is his privilege. But without definitions, the "elevation" of a variety to subspecies, or the "degradation" of a species or subspecies to variety or forma, is a meaningless juggle.

What Vandendries has called geographic races are not races in the sense of Wettstein or in our sense. They are groups of individuals with exactly the same characteristics in every regard, divided lower from each other by intersterility barriers. The example for such "taxa" was among others *Pleurotus ostreatus*. As we now begin to understand, *Pleurotus ostreatus* sensu lato is an accumulation of at least half a dozen different species (Romagnesi 1970), and the delimitation of these was not understood when the different one-spore isolations were shown to be incompatible forty years ago. Consequently, we do not know whether the phenomenon called "geographic races" by Vandendries actually exists in Agaricales (see also Raper 1966).

Much has been said in recent years about the "species concept" of different monographers. It is obvious that the "size" of the accumulation of similar individuals in terms of permissible width of variation, in order to fit into one's image of

a species, varies considerably in different genera. In some genera, where we have "large" species, they are recognized as such only because our knowledge of these groups and the diagnostic characters available are insufficient. This was certainly true in such genera as *Psathyrella* or *Galerina* during the pre-monograph era. But it cannot be denied that in some, particularly older genera, the species are divided by sharper hiatus and the variation inside the species has not reached the status of a linnaeon or "Rassenkreis" or only one subspecies has survived. Only in the most recent groups, in active development and evolutionary progress, will the difference of "species concept" become apparent, whereby the splitters will not recognize "a species in the making" - a subspecies, but call a species the first completed step in evolutionary development. The lumper will look for races which will attach themselves easily to the ancestral or central form as subspecies (varieties). In the present work, a lumper's attitude is taken only where there is enough evidence for the recognition of a subspecies, otherwise a species or a variety is distinguished. In several cases, where the problem needs further study, a once formally proposed species has been enumerated together with others, but in many of these doubtful cases I have added a phrase like "if indeed different from...". In others, especially where the author has not sufficient experience of his own, the doubtful species are simply omitted from the treatment. But slightly over 5000 species are definitely recognized in their respective genera.

### Suborders

Some authors have combined a number of families into suborders or orders. I have (1975, p. iv) discussed the trend of the present era to create unnecessary orders. However some families appear to be more closely related to each other than to others and may be combined into a higher taxon - suborder. This is in my opinion the logical step as long as we wish to maintain the Agaricales as a definite unit within the Basidiomycetes. Bridges between the major taxa in Biota must exist as long as we believe in evolution, and single similarities based on one character alone - apparently the basis of everything that is new in "new systematics" of Basidiomycetes - may be explained by convergence as well as by phylogenetic affinity. Thus, neither the bridges discovered between Gasteromycetes (not only the secotioid or hypogeous ones) and Agaricales and the putative ones claimed to exist between Agaricales and Aphylophorales can destroy the taxonomical entity of taxon Agaricales. This statement should not be understood as implying that the dismemberment of Aphylophorales or even Gasteromycetes into orders is not permissible a priori and in all future, nor does it imply that the hiatus, undoubtedly existing between aphylophoroid groups (Aphylophorales, as we refer to them in this book) and Agaricales is easy to express in short words on the basis of morphological, developmental or chemical characters; nor does it imply that the difference between products of gasteromycetation and those of a slow evolutionary process from or to a functional autobasidium is always easy to determine. Yet, this difference does exist in nature.

If, then, the Agaricales as treated in this book, must be considered a natural taxon, any family or families which differ from others in a sharper and deeper hiatus can be combined into a suborder. I have been hesitant in doing this up to the last edition of *Agaricales in modern taxonomy* (1975) because of the difficulties involved. It seems to me now that these difficulties have been removed not only as far as the Russulaceae (and Bondarzewiaceae) are concerned, but thanks to the chemical investigations of the most recent times, also with regard to the Boletaceae (with Paxillaceae and Gomphidiaceae). The rest of the families, although the extremes (e.gr. *Clitocybe* and *Coprinus*) are apparently far removed from each other, have much more indistinct characteristics, even if the structure of the spore hilum, the number of nuclei per spore, epicutis structure, structure of the hymenophoral trama, or ontogenesis of the carpophores is taken into consideration since all these characters overlap from one family into the other and where this is not the case, we have small families (Amanitaceae, Pluteaceae, Strophariaceae) which are quite homogeneous but quite evidently not of a higher rank than the rest of the families. It is possible that future research will show that some of the families can be elevated to the rank of suborders on the basis of characters not sufficiently appreciated or unknown at present, but the present state of our knowledge does not warrant such a step, let alone a separation of orders.

We must be on our guard against the belief that multiplication of higher taxa and reorganization or upgrading of the old ones is necessarily a step characteristic of modern taxonomy. It is not enough to overemphasize a single character or restrict one's observations to a geographically limited mycoflora. Approximation towards a natural classification requires patient comparative studies on the whole spectrum of characters available now or newly made available, on the largest possible number of taxa of the world mycoflora. The resulting conclusions, sometimes fortified by numerical methods, will produce a more natural classification, and that approach is, I believe, the main characteristic of modern taxonomy.

## **SPECIAL PART**

### **THE FAMILIES, GENERA, AND SPECIES OF THE AGARICALES IN SYSTEMATIC ARRANGEMENT**

## Order: *Agaricales* Clements

*Genera of Fungi*, p. 102, 1909; sensu str. *Rea, Brit. Bas.*, p. xi. 1922.

This order was first proposed in the *North American Flora* in parentheses, and without a diagnosis, but the meaning was the same in Clements's survey, i.e. a valid order name for what was then called the Hymenomycetes. Since the word Agaricales in itself suggests the type family (Agaricaceae) and the type genus (*Agaricus*), it is obvious that we have to use it for the order containing the genus *Agaricus* and the family Agaricaceae, i.e. for the order which we are treating in this book. However, it appears that in their old delimitation neither Hymenomycetes nor Agaricales were acceptable to modern taxonomy. It has been shown before that the division of the homobasidial Basidiomycetes into Gastromycetes and Hymenomycetes is arbitrary, and some may find it preferable to divide the Eu-Hymeniales R. Maire ex Lotsy em. in *Gymnocarpi* (Pers. ex) Pat. and *Gastropileati* Bond. & Sing. (*nom. nud.*) as was (*ad int.*) suggested by us\* as a counterproposal. The word Agaricales, still used as an order, was later emended to contain all of Clements's Agaricales minus the Gasteromycetales and Aphyllophorales of Rea's classification. This is the sense in which it is used here, and this is also the way it is used by most modern taxonomists.

Those who go one step further, restricting Agaricales to the family Agaricaceae\*\* (and perhaps some families they consider closely related) have erected the following orders which we consider synonyms:

*Polyporales* Gäumann, *Vergleichende Morphologie der Pilze*, p. 503. 1926.

*Tricholomatales* Kühner, *Bull. Soc. Linn. Lyon* 48: 613. 1979.

*Pluteales* Kühner, l.c.: 37. 1979.

*Russulales* (Roze) Kreisel, *Grundz. nat. Syst. Pilze*, p. 163. 1969.

*Boletales* Gilbert, *Les Bolets*, p. 105. 1931.

*Amanitales* Jülich, *High. Taxa Basid.* p. 343. 1981. (Locqu. *Synopsis* 1972 *nom. nud.*)

*Bondarzewiales* l.c. p. 344. 1981.

*Cortinariales* Locquin (1977) ex Jülich, l.c. p. 345. 1981.

*Entolomatales* l.c. p. 346. 1981.

The Agaricales must include those genera which because of their obvious similarity to genera of Agaricales belong in the affinity of these genera although they are characterized by a lack of a hymenophore which has come about by an evolutionary process of "cyphephilization" (see chapter VI). We must also include those taxa which are based on gastroid fruiting bodies strictly related to agaricoid genera but having undergone a process of "gasteromycetation" (see chapter V). This necessity makes it difficult to differentiate by simple key characters the Agaricales from the Aphyllophorales (in the first case) and from the Gasteromycetes (in the second case).

\*Bondarzew, A. & R. Singer, *Zur Systematik der Polyporaceae*, *Ann. Myc.* 39: 43. 1941.

\*\*Restricted in the sense of Oberwinkler (Das neue System der Basidiomyceten), Agaricales s.str. excludes even most species of the type genus (*Agaricus*) since the essential characters are given as "...with distal germ pore; basidia... four-spored".

Furthermore, some species of Agaricales now appear to be "lichens", especially in the Tricholomataceae and in *Lactarius* sect. *Panuoidei* (Russulaceae).

Under these circumstances, the question as to whether a Basidiomycete is a member of the Agaricales can often be decided rather on the basis of affinity than by a set of fixed characters. However, by applying this principle, we come to certain results which exclude organisms with any of the following characteristics: (1) All taxa with stichobasidia and with normally septate basidia are excluded; (2) all taxa which never produce a spore print are excluded unless they are gasteromycetation forms (like "Lentodium-forms of *Panus tigrinus*"); (3) all taxa with trimitic hyphal system or with recurring splitting lamella-halves or with leathery lamellae are to be excluded; (4) taxa with spinose hymenophore are to be excluded; also taxa which form a hymenium with basidiospore production on a clavarioid carpophore (unless physalacrioid); (5) fungi with catahymenia are excluded.

Applying the same principle, in the following description of the order Agaricales it is hoped to express not only the classical concept of agarics and boletes but to provide a framework for the recent emendations:

Carpophores annual, not concentrically zonate (unless it where by watery lines or guttate dots or if a latex is present), never effuse-resupinate at maturity but either stipitate-pileate, or pileate with reduced stipe whereby the free pileus assumes an ostreate or cupshaped appearance and sometimes develops a pseudostipe on its sterile side; 0.2 mm to 500 mm in diameter and 0.3 to 500 mm in height, membranous, or fleshy, or fleshy-tough, rarely almost leathery in consistency, and occasionally partly or entirely gelatinous, but never woody or carbonaceous; in most cases with a distinct and well developed hymenophore which is mostly lamellate, more rarely (but still often\*) tubular (porous), rarely venose or absent (and in these cases with all anatomical characters in common with affine lamellate species or genera)\*\*. Species with pseudostipe are always thin, submembranous to flexible-tough, or fleshy-fragile, or partly gelatinous, never thick and corky-tough, but often cyphelloid or pleurotoid, also spathulate, and their spores are often amyloid or pseudoamyloid or the hairs of the sterile surface are pseudoamyloid or beset with calcium oxalate crystals; volva sometimes present; pellicular veil or cortina sometimes present; pseudorhiza, georrhiza, stilboids, arthrospore-bearing carpophores, protocarpic bulbs, carpophoroids, or gastromycetoid carpophores or sclerotia sometimes present.

Spores being shed by the hymenial surfaces to form a spore print under optimal conditions at maturity, small to gigantic (2-48.5  $\mu\text{m}$  long); with evenly rounded outside, or nodulose, nodose-stellate, cruciform, angular; smooth (not ornamented), or irregularly-rough, spinose, echinate, finely echinulate, warty, punctate, longitudinally veined or ridged, or with a fragmentary or complete

\*But not combining tubular hymenophore with short-ellipsoid to subglobose inamyloid hyaline spores and trama nor with short ellipsoid to subglobose spores and very tough leathery to corky consistency nor with cherocytes and/or gloeocystidia and amyloid spores.

\*\*Hymenium developing gymnocarpously, hemiangiocarpously, pseudoangiocarpously, very rarely and exceptionally endocarpously (hemiendocarpously, pseudoendocarpously) see p. 22-25.

network (reticulate), with short interrupted ridges, or with warts connected with very fine anastomosing lines; isodiametric to strongly elongate, most frequently ellipsoid or slightly ovoid, also often subglobose or cylindric with rounded ends, or subfusoid to fusoid, with or without suprahilar depression or appplanation, mostly heterotropic and axillarly asymmetric (i.e. the geometrical axis at the lower end not touching the point of attachment of the hilar appendage), rarely subsymmetric, truncate at the upper end, especially when provided with a germ pore, or non-truncate; wall very thin (beyond the size of measurability by ocular micrometer and oil immersion lens), thin, somewhat thickened (0.5-1.0  $\mu\text{m}$ ), or thick, simple or compound, i.e. either stratose and consisting of an endo- and an episporium, or with imbedded heterogeneous ornamentations (mostly short spines), if stratose more often than not provided with a germ pore or a callus, exceptionally with 2-3 germ pores, amyloid, pseudoamyloid or inamyloid, formed continuously during the life time of the carpophore, or, especially in reviving (light-spored) carpophores, formed only during a short fertile period or several such periods. Aside from basidiospores, chlamydospores are sometimes formed in the hymenophore or in the surface layer of the pileus or the stipe or on protocarpic bulbs or on special synematoid carpophores; arthrospores and conidia are occasionally formed; endospores none (except in *Zerovaemyces*, see p. 518, 857).

**Basidia** - normally autobasidia organized in a euhymenium, clavate to ventricose or constricted to cylindrically attenuate above (false *Urnigera*-type), (1)-2-(3)-4 spored, always chiastic, with the third division usually taking place in the spores or sterigmata before the entering of the (usually) four nuclei (resulting in the second division) into the four spores (one of the resulting nuclei turns back into the basidium to degenerate: species with uninucleate spores), or with the third division taking place in the spores at their maturity (species with binucleate spores); with mostly half-sickle-shaped sterigmata which are not strongly elongate; with or without a clamp between the last tromal or subhymenial cell and the basidium, with or more often without siderophilous granulosity, normally unicellular\*, in the immature stage (without sterigmata) either narrowly clavate or fusoid, thin-walled, rarely thick-walled, generally not sporulating while the hymenium is enclosed and producing a spore print (except in cases of gasteromycetation), rarely forming "bulbils" instead of basidia (bulbillosis), sometimes regularly interrupted by pseudoparaphyses, or with interspersed cystidia of various types, or with pseudocystidia (macrocystidia, gloeocystidia, etc.); the edge of the lamellae or pore walls often heteromorphous or almost heteromorphous, with cheilocystidia.

**Trama** more commonly than not consisting of both fundamental and connective hyphal systems, either di- or amphimitic, or monomitic, frequently with oleiferous hyphae, more rarely laticiferous hyphae, and other elements of the conducting system; fundamental tissue often consisting of sphaerocysts (*Russulaceae*), or of large elements, in the latter case these often coenobial (multinucleate), especially in the stipe; the hyphae sometimes slightly gelatinized with thick walls, or imbedded in a gelatinous mass and then usually thinwalled; amyloid or pseudoamyloid or in-

\*Very rarely and under extraordinary conditions of maturation, a number of basidia in a hymenium may become 1-3-septate like *Auricularia*-basidia (but still chiastic!), for example *Gerronema venustissimum*.

amyloid; hyphae with clamp connections or without them. Hymenophoral trama bilateral, inverse, regular, irregular, or intermixed. Subhymenium present or more rarely absent, either rameous (filamentous), cellular, or intermixed. Hymenopodium either present, or more often absent or very poorly developed.

*Cortical layers* of the pileus and the stipe either little differentiated, or dense, or forming a cutis, or a trichodermium, or a hymeniform layer, or an epithelium, or an "asterostromelloid" or *Rameales*-structure often divided into two to rarely three layers, and sometimes covered by remainders of the velar layer: the outermost layer (mostly the epicutis) often containing dermatocystidia or dermatopseudocystidia, or hair-like bodies; the walls of the hair-like bodies sometimes pseudoamyloid (to amyloid); the walls of other epicuticular hyphae often gelatinized or imbedded in a gelatinous mass.

*Mycelial tomentum* present, or virtually absent at the (insititious) base of the stipe, and if present consisting of thin- to moderately thick-walled, filamentous, multi-septate or very long hyaline or colored hyphae. Mycelium filamentous, rarely forming sclerotia or pseudosclerotia, stilboids, or rhizomorphs, normally divided into two phases, the first resulting from the germination of the spores; the second from the copulation of two hyphae of the haploid mycelium, hyphal cells dicaryotic (or with numerous nuclei), generally haploid, rarely developing a diploid phase.

Parasitic on the roots of trees, herbaceous plants, shrubs, etc., also on trunks of trees, on stems of herbaceous plants and shrubs, even on twigs and leaves of living plants or their fruits, very rarely on animals, much more frequently saprophytically on all kinds of plant débris, even animal débris (hides, bones, hair), often very specialized as to species and organ of the host, also on dung, also on thinly scattered organic matter on sand, rocks, on living trees, pavement, etc., or on the naked earth in pastures, meadows, steppes, tundras, deserts, gardens, roadsides, greenhouses, cellars, often on various artificial matter such as some plastics, sawdust, wooden structures, putty, charcoal heaps, ropes, clothing, etc.; or in close connection with stands of mosses such as *Sphagnum*, *Polytrichum*, etc., or Pteridophyta such as *Pteris*, *Osmunda*, *Blechnum*, etc.; or in symbiosis with Coniferae (mycorrhiza ectotrophic), Dicotyledones (mycorrhiza ectotrophic or ectendotrophic) or Monocotyledones (orchids; mycorrhiza endotrophic), algae (i.e. lichenized). In all zones and continents, altitudes and plant communities, but very rarely truly aquatic. Life cycle never truly dioecic as far as known, but sometimes with a leaf-parasitic or twig-parasitic phase on definite host plants, and a saprophytic sexual phase on forest humus. Fruiting periods mostly highly seasonal in the boreal and in the temperate as well as in part of the tropical zones.

In the Agaricales we distinguish now 18 families with 230 genera with a few additional, apparently good genera (e.g. *Cantharocybe*) not sufficiently known by the present author to insert them in the families where they belong or in the subdivisions of these families.

A survey of the classification as given in the following pages will provide general orientation.

# SURVEY OF THE GENERA OF AGARICALES

## Suborder I. Agaricineae

### Family 1. Polyporaceae

#### Tribus Polyporeae

1. *Polyporus*; 2. *Pseudofavolus*; 3. *Mycobonia*

#### Tribus Lentineae

4. *Phyllotopsis*; 5. *Pleurotus*; 6. *Panus*; 7. *Lentinus*; 8. *Geopetalum*

### Family 2. Hygrophoraceae

#### Tribus Hygrophoreae

9. *Hygrophorus*

#### Tribus Hygrocybeae

10. *Camarophyllus*; 11. *Hygrotrama*; 12. *Neohygrophorus*; 13. *Hygrocybe*; 14. *Humidicutis*

#### Tribus Hygroastreae

15. *Hygroaster*; 16. *Omphaliaster*

### Family 3. Tricholomataceae

#### Tribus Lyophylleae

17. *Lyophyllum*; 18. *Calocybe*; 19. *Asterophora*; 20. *Hypsizygus*

#### Tribus Termitomyceteae

21. *Podabrella*; 22. *Termitomyces*

#### Tribus Tricholomataceae

Subtribus: Laccariinae: 23. *Laccaria*

Subtribus: Clitocybinae: 24. *Clitocybe*; 25. *Lepista*; 26. *Tricholomopsis*

Subtribus: Tricholomatinae: 27. *Tricholoma*

Subtribus: Omphalinae: 28. *Armillariella*; 29. *Arthrosporella*; 30. *Lulesia*; 31. *Arrhenia*; 32. *Leptoglossum*; 33. *Omphalina*; 34. *Gerronema*; 35. *Callistosporium*; 36. *Pleurocollybia*; 37. *Lactocollybia*; 38. *Macrocytidia*; 39. *Fissolimbus*; 40. *Asproinocybe*

Reduced series: 41. *Cyphellostereum*

### Tribus Leucopaxilleae

Subtribus: Porpolomatinae: 42. *Cantharellula*; 43. *Pseudoarmillariella*; 44. *Pseudoomphalina*; 45. *Pseudoclitocybe*; 46. *Clitocybula*; 47. *Porpoloma*  
Subtribus: Leucopaxillinae: 48. *Leucopaxillus*; 49. *Melanoleuca*

### Tribus Biannularieae

50. *Catathelasma*; 51. *Armillaria*

### Tribus Collybieae

52. *Trogia*; 53. *Pleurocybella*; 54. *Cheimonophyllum*; 55. *Anthracophyllum*; 56. *Collybia*; 57. *Neoclitocybe*; 58. *Marasmiellus*; 59. *Micromphale*; 60. *Campanella*  
Reduced series: 61. *Cymatella*; 62. *Skepperiella*; 63. *Mniopetalum*; 64. *Cyphella*; 65. *Phaeodepas*; 66. *Calyptella*

### Tribus Resupinateae

67. *Resupinatus*; 68. *Agaricochaete*; 69. *Hohenbuehelia*

Reduced series: 70. *Stigmatolemma*; 71. *Stromatocyphella*; 72. *Aphyllotus*

### Tribus Panelleae

73. *Tectella*; 74. *Dictyopanus*; 75. *Panellus*

### Tribus Marasmieae

Subtribus: Oudemansiellinae: 76. *Oudemansiella*; 77. *Mycenella*; 78. *Physocystidium*; 79. *Strobilurus*

Subtribus: Marasmicinae: 80. *Marasmius*; 81. *Rimbachia*; 82. *Physalacria*; 83. *Deigloria*; 84. *Gloiocephala*; 85. *Palaeocephala*; 86. *Manuripia*; 87. *Epicnaphus*; 88. *Hymenogloea*

Subtribus: Crinipellinae: 89. *Crinipellis*; 90. *Chaetocalathus*; 91. *Amyloflagellula*

Reduced series: 92. *Lachnella*; 93. *Flagelloscypha*

### Tribus Myceneae

94. *Hemimycena*; 95. *Delicatula*; 96. *Pegleromyces*; 97. *Amparoina*; 98. *Mycena*; 99. *Hydropus*; 100. *Filoboletus*; 101. *Dennisiomyces*; 102. *Dermoloma*; 103. *Xeromphalina*; 104. *Baeospora*; 105. *Resinomyces*; 106. *Fayodia*; Reduced series: 107. *Cellypha*; 108. *Pleuromycenula*; 109. *Mycoalvimia*

### Tribus Pseudohiatuleae

110. *Flammulina*; 111. *Pseudohiatula*; 112. *Cyptotrama*; 113. *Callistodermatium*

### Tribus Rhodoteae

114. *Rhodotus*

## **Family 3. Amanitaceae**

115. *Amanita*; 116. *Limacella*

## **Family 4. Pluteaceae**

117. *Volvariella*; 118. *Chamaeota*; 119. *Pluteus*

## **Family 5. Agaricaceae**

### Tribus Leucocoprineae

120. *Clarkeinda*; 121. *Chlorophyllum*; 122. *Volvolepiota*; 123. *Macrolepiota*; 124. *Leucoagaricus*; 125. *Leucocoprinus*; 126. *Sericomyces*

### Tribus Agariceae

127. *Agaricus*; 128. *Cystoagaricus*; 129. *Crucispora*; 130. *Melanophyllum*; 131. *Micropsalliota*

### Tribus Lepioτae

132. *Smithiomycetes*; 133. *Hiatulopsis*; 134. *Janauaria*; 135. *Cystolepiota*; 136. *Lepiota*; 137. *Chamaemyces*

### Tribus Cystodermateae

138. *Cystoderma*; 139. *Phaeolepiota*; 140. *Dissoderma*; 141. *Squamanita*; 142. *Pseudobaeospora*; 143. *Ripartitella*; 144. *Horakia*

## **Family 6. Coprinaceae**

### Subfamily Coprinoideae

145. *Coprinus*

### Subfamily Psathyrelloideae

146. *Macrometrula*; 147. *Psathyrella*

### Subfamily Panaeoloideae

148. *Panaeolina*; 149. *Panaeolus*; 150. *Copelandia*; 151. *Anellaria*

## **Family 7. Bolbitiaceae**

152. *Conocybe*; 153. *Galerella*; 154. *Pholiotina*; 155. *Descolea*; 156. *Bolbitius*; 157. *Agrocybe*

## **Family 8. Strophariaceae**

### **Subfamily Stropharioideae**

**158. *Stropharia*; 159. *Naematoloma*; 160. *Psilocybe*; 161. *Melanotus***

### **Subfamily Pholiotoideae**

**162. *Pholiota*; 163. *Kuehneromyces*; 164. *Pachylepyrium*; 165. *Pleuroflammula*;  
166. *Phaeomarasmius***

## **Family 9. Cortinariaceae**

### **Tribus Inocybeae**

**167. *Inocybe*.**

### **Tribus Hebelomiteae**

**168. *Hebeloma*; 169. *Hebelomina*; 170. *Alnicola***

### **Tribus Cortinarieae**

**171. *Rozites*; 172. *Cuphocyste*; 173. *Cortinarius*; 174. *Dermocybe*; 175. *Leucocyste*;  
*corticarius*; 176. *Stephanopus*; 177. *Gymnopilus*; 178. *Pyrrhoglossum*; 179.  
*Phaeocollybia*; 180. *Galerina***

## **Family 10. Crepidotaceae**

**181. *Tubaria*; 182. *Melanomphalia*; 183. *Simocybe*; 184. *Crepidotus*; 185. *Pleurotellus***

**Reduced series: 186. *Episphaeria*; 187. *Phaeosolenia*; 188. *Pellidiscus*; 189. *Chromocyphella***

## **Family 11. Entolomataceae**

**190. *Clitopilus*; 191. *Rhodocybe*; 192. *Entoloma***

### **Suborder II. Boletineae**

## **Family 1. Paxillaceae**

**193. *Lampteromyces*; 194. *Omphalotus*; 195. *Hygrophoropsis*; 196. *Paxillus*; 197.  
*Phyllobolites*; 198. *Neopaxillus*; 199. *Ripartites***

**Family 2. Gomphidiaceae**

200. *Cystogomphus*; 201. *Gomphidius*; 202. *Chroogomphus*

**Family 3. Boletaceae**

Subfamily Gyroporoideae

**203. *Gyroporus***

Subfamily Gyrodontoideae

**204. *Paragyodon*; 205. *Phlebopus*; 206. *Gyrodon*; 207. *Meiorganum***

Subfamily Suilloideae

**208. *Psiloboletinus*; 209. *Boletinus*; 210. *Suillus*;**

Subfamily Xerocomoideae

**211. *Phylloporus*; 212. *Xerocomus*; 213. *Tubosaeta***

Subfamily Boletoideae

**214. *Chalciporus*; 215. *Pulveroboletus*; 216. *Boletus*; 217. *Boletellus*; 218. *Phylloboletellus*; 219. *Leccinum*; 220. *Xanthoconium*; 221. *Veloporphyrillus*; 222. *Porphyrellus*; 223. *Tylopilus*; 224. *Boletochaete*; 225. *Fistulinella*; 226. *Astroboletus***

Subfamily Strobilomycetoideae

**227. *Strobilomyces***

Suborder III. Russulineae

**Family 1. Bondarzewiaceae**

**228. *Bondarzewia***

**Family 2. Russulaceae**

**229. *Russula*; 230. *Lactarius***

**Key to the suborders**

A. Trama of the carpophores homoiomerous throughout, if dimitic - without laticiferous hyphae, with clamp connections, rarely without clamp connections and with smooth, inamyloid spores, otherwise monomitic

B. Hymenophore often tubular and then tube trama more or less distinctly bilateral in young carpophores and spores always ± pigmented (ochraceous-yellow, brown, melleous-olive, porphyry or dull pink to pink, or gray to blackish in fresh spore print); if hymenophore lamellate, pigments of the carpophore and/or mycelium of the variegatic acid type or derivatives (or otherwise related to pigments commonly found in boletes) and lamellae ± decurrent\*, if spore print white or yellowish white - trama soft and subgelatinous, or lamellae repeatedly forked or carpophores luminescent; spores generally uninucleate and cyanophilic; basidia not siderophilous, or if so, of the Gigas-type; spore hilum mostly of the open-pore type, wall rarely (if ever) truly amyloid, but often pseudoamyloid; tramal system monomitic

BOLETINEAE p. 718

B. Hymenophore unfrequently tubular and then tube trama not bilateral and spores scarcely or not pigmented; in the majority of cases (except in Polyporaceae) the hymenophore is lamellate, but at times it is absent; spores rarely at the same time well pigmented and uninucleate; partial luminescence occurring generally only in species with amyloid spores; basidia siderophilous or not; spore hilum of the nodulose or the open-pore type; tramal system monomitic, dimitic, or amphimitic

AGARICINEAE (below)

A. Trama of the carpophores at least in part heteromerous or, if homoiomerous: dimitic and/or with laticiferous hyphae, with amyloid spore ornamentation, without clamp connections, root-parasitic

RUSSULINEAE p. 802

### Subordo AGARICINEAE Fr.

*Syst. Orb. Veg.* p. 65. 1825 (Agaricini); *Rea, Brit. Bas.* p. 55. 1922.

*Characters:* Those indicated in the key above.

*Type genus:* *Agaricus* (Agaricaceae)

#### Key to the families

##### 1. Basic key (I)

- A. Trama of the hymenophore bilateral or inverse.
- B. Trama of the hymenophore of the primordium regular, of adult lamellae bilateral with inflated hyphae; or trama of the primordial hymenophore bilateral-divergent, of the adult lamellae as above, or inverse; hymenophore always well developed, lamellate, free; spore print white, dull pink, rarely somewhat greenish; context of pileus and stipe thick and fleshy. Succession of the primordium-development of the pileocarpic type; elements of the stipe generally distinctly cenocytic.
- C. Spores in print mostly white or whitish, rarely somewhat pinkish or greenish, acyanophilous or almost so; adult lamellae with bilateral trama structure. Hilum typically of the nodulose type.
- AMANITACEAE, p. 442
- C. Spores in print a dull pink, distinctly cyanophilous with cotton blue lactic acid; adult lamellae with inverse hymenophoral trama; hilum of the open-pore type.
- PLUTEACEAE, p., 454
- B. Trama of the hymenophoral trama bilateral-divergent and remaining so in the young carpophore, never inverse. Hymenophore always well developed, either tubulose or, if lamellate (not venose), subfree or not free; spore print color as above or different; context of pileus and stipe thick and fleshy to thin and submembranaceous, also often soft-subgelatinized. Succession of the

\*In those forms where no pigment analyses are available, the spore print is not white, the spores always pigmented, the carpophores always clitocyboid or luminescent, the spores ornamented and globose to subglobose, or if smooth, illudins are present if not subglobose, they have red pileus with an ixocutis, the stipe annulate, and the hymenium with pseudocystidia. Chemically poorly known forms, here attached to the Boletineae, are also keyed out in the Agaricineae, if they do not conform with the above characterization.

primordium development pileo-stipitocarpic or stipitocarpic; elements of the stipe mostly with two or few nuclei.

D. Spore print white; spores smooth, inamyloid, acyanophilous; basidia long: the majority (5-5.5-6(6.5) times as long as the longitudinal axis of the spores; hymenophore lamellate, lamellae adnate to subdecurrent or decurrent, rather thick and waxy, often rather distant; fleshy carpophores often veiled, pileus and/or stipe often glutinous (but not always!). All species growing in obligatory ectomycorrhizal symbiosis with Fagales, Pinaceae, *Tilia*

**HYGROPHORACEAE (*Hygrophorus*), p. 190**

D. Spore print either not white, or spores amyloid or pseudoamyloid or cyanophilous; or else basidia considerably shorter than indicated above; hymenophore lamellate, the lamellae not thick and waxy and subdistant to distant. Obligatory or facultative ectomycorrhizal fungi, or not (often parasitic, endomycorrhizal, or parasitic)

E. Tramal system monomicic

**TRICHOLOMATACEAE (p.p.) p. 209**

E. Tramal system not monomicic (see Key II)

A. Hymenophoral trama neither bilateral (excepting in the strictly primordial stage) nor inverse, but regular or irregular, or hymenophore absent

F. Spores at the same time angular or longitudinally striped (by narrow veins or flattened stripes causing the spores to appear subangular in polar view) and inamyloid, cyanophilous, stramineous to pale pinkish in NH<sub>4</sub>OH and dull pink, rarely livid gray in print; hilum nodulose

**ENTOLOMATACEAE, p. 698**

F. Spores not at the same time angular (from any side) and inamyloid, cyanophilous and dull pink in print; if the spores are angular or otherwise not terete, they are white or brown in print.

G. Spore print pure white, cream color, light ochraceous yellowish, cream-salmon to dirty pink, light pink, light greenish (and then often turning to reddish by dehydration), also pale citrine, light salmon orange, pale livid-violet to livid-pallid; under the microscope (oil immersion) spore wall usually hyaline; hymenophore lamellate, tubular, venose, or absent (see Key II)

G. Spore print deeper colored; hymenophore lamellate, rarely (in cyphelloid forms) absent, but never tubular (Key III)

## Key II

### (Pale-spored families)

A. Hyphal system mono-, di- or amphimitic; spores  $\pm$  elongated (cylindric-oblong, sausage-shaped, cylindric-fusoid, fewer subelliptic to oblong or subfusoid but if  $Q < 2.1$  spore print livid-violet or tramal system not monomicic) and smooth, inamyloid and quite hyaline under the light microscope (KOH), trama of the pileus (and stipe if it is differentiated) somewhat tough to distinctly tough, at least in age (because of the presence of many thickwalled hyphae) not gelatinized in a definite gelatinized (upper) zone; hymenophore if present, often tubular or with veins, or lamellate. Stipe often lateral to eccentric or concrecent polypilous, may also be entirely absent; covering layers of pileus and stipe devoid of broom cells, hymeniform or epithelial structures or acanthocysts; clamp connections mostly present. Mostly on dead wood or parasitizing on the trunk or the roots of trees, also on imbedded, buried wood, rarely on grass roots, sometimes on umbelliferous plants: "Polypores" and *Pleurotus*-like genera

**Polyporaceae, p. 163**

(Lamellate forms, often with serrate edges, with clamp connections and rough, short, amyloid spores and without latex which may key out here are *Lentinellus* and belong in the Aphyllophorales. (see p. 847)

A. Hyphal system monomicic (as far as known, occasionally dimitic in the stipe but then spores short with  $Q < 2$ ); spores as above or different; not combining all the characters as enumerated above. Species with tubular hymenophore have mostly amyloid, smooth spores.

B. Lamellae rather thick and waxy, never quite free; often subdistant or distant; basidia all or most over 5 times longer than the long axis of the spores. Fleshy, non-pleurotoid carpophores, most frequently growing on the ground or in deep moss. Spore print generally white and spores acyanophilous, mostly not pseudoamyloid, and no pseudoamyloid hairs present, rarely amyloid (and then the context turns red in KOH), spores star-shaped-spinose, or more frequently not and then

quite smooth, rarely with indistinctly heterogeneous but rather thin to thin spore wall, mostly gymnocarpic, more rarely monovelangiocarpic, exannulate. Type of succession in primordial development: stipitocarpic (Reijnders). The carpophores are often bright (red, yellow, etc.) pigmented and the stipe and/or pileus with a glutinous covering; they are not reviving after drying out, nor do they have cherocytes (or similar diverticulate hyphae) or broom cells; spores uninucleate or binucleate; hyphae inamyloid; basidia without siderophilous granulation; hilum of spores of the nodulose type.

*HYGROPHORACEAE* (excl. *Hygrophorus*), p. 190

B. Lamellae mostly thin and basidia less than or up to 5 times longer than the long axis of the spores; if the lamellae are thick and the basidia long, the characters enumerated above are not all correlated.

C. Lamellae free; either spores pseudoamyloid or epicutis hymeniform or an epithelium; development of the carpophore primarily angiocarpous; volva sometimes, veil always present, annular veil mostly present; basidia without siderophilous granulation; spores sometimes with a distinct germ pore and a metachromatic endosporium in cresyl blue mounts.

*AGARICACEAE* (*Leucocoprinae*, *Lepioteae*), p. 465

C. Lamellae subfree to decurrent, more rarely free (and then fungi do not combine the characters indicated above).

D. Veil present, habit non-pleurotoid or scarcely so, and having *either* and an epithelium on both pileus and stipe, *or* a protocarpic tuber from which the stipe rises *or* distinctly ornamented spores *or* a hymeniform epicutis and light ochraceous spore print; siderophilous granulation constantly absent; squamulose surface on the pileus frequently present; hilum of spores generally of the open-pore type

E. Both spores and epicuticular elements pigmented, the latter by a well incrusting pigment; pileus <70 mm broad; cheilocystidia present, pleurocystidia absent; spores quite smooth (see Key III)

E. Not both spore wall and epicuticular elements pigmented or pileus more than 70 mm broad or both cheilocystidia and pleurocystidia absent

F. Germ pore none

*AGARICACEAE* p.p., p. 465

F. Germ pore present (see Bolbitiaceae)

D. Either no veil is present or if a veil is present, there is no correlation of the above-mentioned characters

G. Spores pseudoamyloid or at least cyanophilous, smooth; habit clitocyboid or pleurotoid, with repeatedly forked lamellae or with luminescent carpophores; trama fleshy, often remarkably soft; cystidia none; clamp connections present (see Paxillaceae p. 719)

G. Not combining these characters

H. Spore print off white (tending to salmon or "cork" (Maerz & Paul) and spore wall slightly pigmented when seen under oil immersion in KOH; habit pleurotoid; trama soft, thin and not gelatinized; clamp connections absent (see Crepidotaceae)

H. Not as above

I. Spore print off white; spore wall slightly pigmented when seen under oil immersion in KOH, heterogeneous (with ornamentation XI), inamyloid; clamp connections present (see Crepidotaceae)

I. Spore print white or pinkish or palest livid or cream to pale cinnamon; spore wall heterogeneous or homogeneous (light microscope); spores amyloid, pseudoamyloid or inamyloid; clamp connections present or absent

J. Spores with spines, star-like, acyanophilous, inamyloid; hyphae without clamp connections; habit omphaliod; epicutis - a cutis (see Hygrophoraceae)

J. Not combining these characters

K. Spores extremely finely punctulate from a weak ornamentation of type XI, inamyloid; habit and colors of *Hygrocybe*; epicutis - an ixocutis, clamp connections present (see Hygrophoraceae); habit and colors of Tricholoma; spores amyloid (see "L" below)

K. Not combining these characters

L. Metuloids of the *Inocybe*-type present or a marginate bulb at the base of the stipe, or spores pseudoamyloid. Veil - a cortina or development

at least monovelangiocarpous. Pseudoamyloid hairs not present on the surface of pileus and stipe. Spores binucleate with open pore hilum (EM) (see Key III)

- L. Spores usually uninucleate when just discharged and with nodulose (EM) hilum, more rarely with open-pore type hilum (and then either basidia with siderophilous granulation or carpophores with hymeniform epicutis and non-metuloid cystidia, or termitophilous fungi without clamp connections and with pinkish spore print) or with binucleate spores (and then metuloids absent, spores not pseudoamyloid, and stipe without margined bulb) but more generally uninucleate

*TRICHOLOMATACEAE* (most tribes), p. 209

### *Key III*

(Dark-spored families)

- A. Pileus epicutis hymeniform, rarely an epithelium; spores mostly (but not always!) with a truncate germ pore with a complex wall; elements of the epicutis mostly not conspicuously pigment-incrusted, at least not in their upper portion if the spore print is cinnamon to ochraceous or tobacco brown. Hymeniform or epithelial covering of the pileus continuous (discontinuous only if either pleurocystidia present or spores with a truncate germ pore or verrucose and black in print); spore ornamentation of type XI never observed. Fungi not obligatorily mycorrhizal
- B. Spore print ferruginous to fuscous-tobacco-brown or deep ochraceous. Epicutis always hymeniform (sometimes discontinuously so but then either without clamp connections or with pleurocystidia, or spores broadly truncate)
- BOLBITIACEAE*, p. 540
- B. Spore print violet-fuscous, purple-brown, dull fuscous-bister, dark fuscous to nearly or quite black, cinnamon brown or reddish ochraceous, ocher-red; if without a broad, truncate germ pore, then part of the spore pigment easily dissolving in concentrated  $H_2SO_4$ ; epicutis hymeniform or an epithelium, if both conditions indistinct, the spore print is black
- COPRINACEAE*, p. 514
- A. Epicutis of the pileus neither hymeniform nor epithelial unless the spores are devoid of a broad, truncate germ pore or unless obligatory ectomycorrhiza is formed, or a spore ornamentation of type XI is present.
- C. Lamellae in section not wedge-shaped, with parallel sides and numerous pseudoparaphyses; hymenophore generally more or less deliquescent, at least towards the edges of the lamellae, forming a deep fuscous to black inky emulsion at maturity; pigment of spore wall soluble in concentrated  $H_2SO_4$
- COPRINACEAE* (Coprinoideae), p. 515
- C. Lamellae in cross-section wedge-shaped, never deliquescent; pseudoparaphyses rare and few, or none
- D. Either the spores are asymmetrical or cross-shaped or the lamellae are quite free, or both. Spore print brown, violet brown or sepia, more rarely red (when dehydrated); veil present, often annuliform, even double
- AGARICACEAE* (Agaricaceae), p. 482
- D. Spores generally neither asymmetrical (excepting axially asymmetrical) nor cross-shaped but often punctate, ridged, verrucose, nodose-sinuate, starshaped. Lamellae rarely free. Spores in print as indicated above or differently colored. Veil present, sometimes double, or absent
- E. Spores constantly quite smooth in the light microscope under oil immersion (there is also no trace of a plage line) with even outline (never nodulose-sinuate nor star-shaped); clamp connections constantly present; epicutis either a cutis or ixocutis or a trichodermium, or with hyphal strands bundled together and forming scales, or of spherocyst chains with strong pigment incrystation; chrysocystidia or oleocystidia or other, even thick-walled pleurocystidia often present and spore print deep lilac, lilac, violet brown, tobacco brown, clay, ferruginous brown; only if here is a strongly pigment-incrusted epicutis or if the epicutis contains numerous spherocysts, is the spore print at times ochraceous to cinnamon-ocher but then there are no pleurocystidia. Spores either with germ pore or without; spore walls always layered bi- to tristratous but homogenous. Fungi all not ectomycorrhizal. Development: frequently bivelangiocarpous, never gymnocarpous carpophores not mycenoid
- STROPHARIACEAE*, p. 556

- E. Not combining all the characters enumerated above
- F. Habit clitocyboid; spores with short rod-shaped or verrucose ornamentations (type VI mostly), often globose or subglobose, ± brown in print (see Paxillaceae, cf key II, "I".)
- F. Either not clitocyboid or with different spores
- G. Obligatorily ectomycorrhizal fungi which cannot easily be grown on standard agar media like potatoe dextrose agar without addition of growth substances; stipe central. (Species with nodose-sinuose spore outline or with stellate or angular spores and with metuloids of the *Inocybe*-type belong here; likewise most large fleshy, soil-inhabiting fungi of the temperate forest, most of them with rough ferruginous spores, and without cheilocystidia, belong here)

*CORTINARIACEAE*, p. 595

- G. Not ectomycorrhizal (but sometimes endomycorrhizal or root-parasitic); stipe central, eccentric or lateral, or absent.

- H. Spores rarely quite smooth and then pseudoamyloid and/or with firm double wall and germ pore or at least a callus, either with pleurocystidia or spores reaching over 10  $\mu\text{m}$  in length, never with relatively thin, relatively light colored, easily collapsing wall; mostly somehow ornamented but not with a distinct echinulate or punctate ornamentation which under the light microscope corresponds to type XI, but rather by a warty, warty-ridged or finely punctate or marbled exosporial ornamentation, spores in print mostly ferruginous brown to bright ferruginous even orange ferruginous. (If there is little veil or none and a long georrhiza, spores ferruginous and ornamented, pileus viscid, choose this alternative)

*CORTINARIACEAE* (non-ectomycorrhizal genera of the Cortinarieae), p. 595

- H. Spores either quite smooth (and then always with distinctly pigmented wall), or if not, they are ornamented by a general unevenness of the (easily collapsing) wall, or else punctate (rarely more strongly verrucose) with an ornamentation of type XI (which in EM section differs from the "Cortinarius-type" by showing individualized or paired, fully erect columns. (cylinders or narrow cones, which are hollow), or ridges, under oil immersion in the light microscope they appear to have deeper colored or denser short columns perforating the epi-sprium or rising from it, and imbedded in a hyaline outer layer beyond which they may or may not project; spores in print all shades of brown but not a bright nor orangy ferruginous color, sometimes reaching an olive black or a yellow-ochraceous shade, but also often tobacco brown or ochraceous cinnamon, more rarely some kind of cream ("cork", salmon color). If the spores are ornamented, they never have a true plage, and the hyphae of the centrally stipitate forms have clamp connections. Habit variable

*CREPIDOTACEAE*, p. 678

## POLYPORACEAE (Fr.) Fr.

*Epicr.* p. 408 (Polyporei, as ordo) 1838; Corda, *Icon. Fung.* 3: 49. 1839; Cohn, *Hedwigia* 11: 17. 1872, em.

*Type genus: Polyporus* Micheli ex Fr.

*Syn:* *Polyporei* Fr., *Orb. Veg.* p. 79. 1825 (subordo)

*Pleurotaceae* Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 20. 1927 ex Kühner & Romagnesi in Kühner, *Bull. Soc. Linn. Lyon* 49: 184. 1980

*Lentinaceae* Van Overeem, *l.c.* p. 20

*Mycoboniaceae* Jülich, *Higher Taxa Basid.* p. 380. 1981

*Geopetalaceae* Jülich, *l.c.* p. 371

*Characters:* Pileus usually rather fleshy but especially in age becoming fleshy-tough, pilose squamose, or fibrillose, but also glabrous, generally not with gelati-

nized surface layers; stipe central or more often eccentric, lateral, or absent; veil present or absent (but no basal volva); lamellae or tubes present, or radial veins or a smooth hymenial surface bearing the hymenium; spore print white, cream, pale lilac-livid, or pink. Spores elongated, rather narrow, smooth, with rather thin wall and without a germ pore or callus, mostly cylindric, fusoid-cylindric, oblong-cylindric, and frequently appearing sausage-shaped when seen laterally, inamyloid, weakly cyanophilous. Basidia normal (neither extremely long nor extremely narrow, mostly 4-spored, chiastic, clavate) but occasionally thick walled (sclerified) basidia present. Cystidia present or absent, often metuloid, cheilocystidia frequently developed. Hymenophoral trama irregular but initially often regular, rarely bilater al, sometimes persistently regular, never inverse, its hyphae often thick-walled, inamyloid, sometimes amyloid in the stipe-rind, not thin-walled and imbedded in a gelatinous mass. Trama of pileus and stipe mono-, di-, or amphimitic, i.e. with generative and often either skeletal or ligative (binding) hyphae the latter as transformed ends of skeletal hyphae, laticiferous hyphae absent, but often some oleiferous hyphae scattered, clamp connections usually numerous (except in *Lentinus sulcatus*). Cortical layers not hymeniform nor epithelial, but otherwise rather variable. *Mylitta* (*Pachyma*) type sclerotia, pseudosclerotia, carpophoroids, gasteromycetoid mutations, sterile antler-like bodies often formed under certain environmental conditions, and the hymenophore, by gasteromycetation, gleba-like-convoluted. - Habitat on wood, living as well as dead, also (more rarely) on living or dead roots or immersed wood, much more rarely on grass roots, charcoal, etc., even occasionally on bones.

**Limits:** The limits of the Polyporaceae in the restricted sense as used here, are not difficult to trace. The Polyporeae, i.e. the tubulose, pore-bearing genera are evidently different from any pore-bearing Agaricales such as *Dictyopanus*, *Filoboletus* etc. and should neither be confused with the Scutigeraceae and Coriolaceae of the Aphylophorales; the former having quite different spore characters and the latter being tougher (mostly trimitic) and frequently characteristically concentrically zonate. If the Coriolaceae are lamellate, the lamellae are leathery or corky. Thus, the lamellate genera (Lentineae) of the Polyporaceae have nothing in common with the Aphylophorales, not even with the genus *Lentinellus*, so long confused with *Lentinus* because of the serrulate gill edge; but the spores are here of an entirely different type (and so are the cystidia).

The Lentineae differ from the Tricholomataceae by the combination of characters as indicated in the family key and the family description. It is true that both pleurotoid and elongate-spored Tricholomataceae and Collybieae (the tribus which seem to come closest to the Polyporaceae), Resupinateae and Panelleae exist. There is, however, no true affinity between the latter two groups and the Lentineae. Even as far as *Lampteromyces*, *Omphalotus* and *Clitocybe* are concerned, we cannot see any true transition or find any difficulty in separating them from *Pleurotus*. In *Lampteromyces* on one hand, and *Pleurotus ostreatus* on the other, the habit is similar (pleurotoid) but otherwise these fungi are quite different anatomically and chemically. *Omphalotus* is likewise quite different in these regards. Some lignicolous *Clitocybe* and *Neoclitocybe* species may well pass as fleshy or small *Pleurotus*,

especially where the spores are elongated, but differ in the type of pseudocystidia or the much thinner walls of even the mature hyphae. The spores are white in a print, and the fungus is so visibly related to species with short-ellipsoid spores as *C. lignicola*, *C. lignatilis* and other pleurotoid Tricholomataceae that I cannot share A. H. Smith's opinion that the genus *Pleurotus* is more closely related to the Clitocybeae than to the Polyporeae, an opinion I ascribe to his tendency to admit an extremely wide genus concept in *Pleurotus*, a tendency driven to its extremes by Corner (1981). On the other hand, Corner is right in reuniting *Nothopanus eugrammus* with *Pleurotus* as we have already done (Singer & Kuthan, *Česká Mykologie* 34: 71-72. 1980) three years earlier. He is also right in transferring *Clitocybe* sect. *Augustinenses* to the tribus Lentineae (his genus *Lentinus*, our *Pleurotus*) on the basis of a revision of the type.

Corner (1981) as well as Smith is correct in stressing the fact that some Tricholomataceae are indeed close to the Polyporaceae in some regards, enough, in fact, to discredit the recent attempts to separate the latter in a special order (Polyporales) from the Agaricales (or Tricholomatales) proper (Kreisel 1968, Oberwinkler et al.). The hiatus between Lentineae (Polyporaceae) and Clitocybeae (Tricholomataceae) is undoubtedly not on the same level of depth and sharpness as that between Agaricinae and Russulinae, thus not of the importance that would justify an order or suborder.

Such species as that described by Corner as *Pleurotus problematicus* are indeed problematic and, taken at face value, would suggest that certain species of Tricholomataceae have indeed dimitic hyphal systems in Corner's terminology. I have not studied this species. If correctly described, it would appear to be intermediate between Lentineae and Tricholomataceae.

On the other hand, the Lentineae and Polyporeae are obviously and undoubtedly very closely related. The anatomy of the hymenophoral trama represents three different types in the Lentineae which all reappear in the Polyporeae. The various representatives of both tribus cannot be distinguished macro- or microscopically, if the configuration of the hymenophore is not actually seen. Some species of the *Favolus*-group of *Polyporus* have the characteristic pale lilac-livid spore print of *Pleurotus ostreatus* and allies. The development and anatomical characters of *Lentinus* and *Polyporus* have been compared by Kühner (1928) and were found to be very similar. Donk has likewise indicated his conviction that both groups are indeed related. Nevertheless, he argues that it is necessary to study the tramal systems of both tribus in order to come to a conclusion. This has now been done, and we find that in both tribus, mono-, di- and amphimitic trama is represented. The well-known antler-like carpophoroids or telostipes of *Lentinus lepideus* produced in cellars and mines are formed because of an inability to form pilei in darkness. This inability was demonstrated experimentally in "*Pleurotus squamulosus*" by S.O. Alasoadura and in *Polyporus brumalis* by Plunkett (*Ann. Bot. s.n.* 20: 563-586, 1956). This is interesting since the response to lack of light in other Agaricales is frequently weaker or of a different nature (see also chapter III, B).

A further confirmation of the close affinity between Polyporeae and Lentineae has

been indicated by Pouzar (1972). The elements of the covering of the stipe, especially the basal portion of it (the "incrusted layer") are often amyloid in *Polyporus* as well as in the related agaricoid species *Lentinus suavissimus* and *Panus tigrinus*.

Furthermore, we find that the carpophores of *Polyporus mylitta* Cke & Mass., *P. sapurema* Moeller, *P. cabocli* Souza & Araujo, "*Poria*" *cocos* Wolf, and *Pleurotus tuberregium* (Fr.) Sing. germinate from "Mylitta-" sclerotia (*Pachyma* Fr.), which appear to be restricted, in Basidiomycetes, to the family Polyporaceae s.str.! These sclerotia are hardly distinguishable from one species to another unless the carpophores have been grown from them.

The conclusion that the Polyporeae and the Lentineae are closely related and cannot be put in different families, let alone orders, is inescapable and has been drawn for part or all of the genera involved, from Fries ("Favoli veri absolute agaricini, Polypori autem favoloidei ab hoc genere neutiquam separari debent") and Van Overeem ("Die Gattung *Polyporus* gehört eher zu den Agaricales") to Kühner (1929, 1963, 1981), Donk (1964), Corner (1953, 1981), Singer (1951), Locquin (1957), Kreisel (1961), and Pegler (1977).

If the Lentineae + Polyporeae form a single unit on the family level, what should be done with them? Three solutions are possible. The first would be a transfer of the whole family to the Aphyllophorales. This solution has against it: (1) the relatively close similarity between *Pleurotus* and *Lentinus* on one hand and some Clitocybes on the other; the hiatus being approximately on the family level in Agaricales, but it is not sufficiently large to separate two orders. (2) In the Polyporaceae, we have two features which are characteristically Agaricales-features: first of all - veil, secondly - mutations which lead to gasteromycetation. The genus *Microporellus*, supposedly dimitic and like *Polyporus* sensu stricto, is a typical trimitic Coriolaceae-genus as described and frequently observed in the American tropics and subtropics. The fact that it as well as other genera of that group have a stipe or pseudostipe does not reflect their affinities. (3) the fact that the Polyporeae or Polyporoideae (with *Polyporus* sensu stricto as the type) fall into a very definite, well defined group, separated from the rest of the "polypores" by several important characters when they are analysed according to the scheme elaborated by Nobles (1959, and in Petersen 1971). *P. arcularius*, *brumalis*, *elegans*, *melanopus*, *platensis*, *radicatus*, *squamosus*, *tuberaster* (type of the genus *Polyporus*!), *varius* have been tested by her - and we may add that *P. coronatus* and *P. maculatissimus* fall into the same pattern as well as the numerous species of Lentineae thus far checked - and are characterized by the following cultural characters: Extracellular oxidase positive; clamp connections in mycelium present; hyphae differentiated to form fibre-hyphae (but not differentiated to form cuticula-cells closely packed together into a pseudo-parenchyma); hyphae differentiated through formation of numerous short branches, hooked or recurved or thick-walled nodules interlocked to form a plectenchyma (but not differentiated to form numerous interlocked, contorted, incrusted hyphal tips).

The second possibility is to include the Polyporaceae in the Agaricales. The only

serious difference between this and the classical families of the Agaricales is the fact that the latter are mostly - according to my experience - monomitic in the original definition as here accepted whereas there are dimitic (in the original definition) species both in the Polyporeae and the Lentineae (and in both groups both dimitic and amphimitic, i.e. skeletal and ligative hyphae do occur).

I consider this discrepancy of minor importance and believe it should not stand in the way of an incorporation of the Polyporaceae in the Agaricales inasmuch as in *Lactarius* sect. *Panuoidei*, the subiculum and lower part of the stipe are dimitic with skeletals, and the Bondarzewiaceae are a family of the Agaricales and dimitic.

The third possibility for a solution of the taxonomic problem has been proposed by Kreisel (1969). In cases of "intermediate" taxa it is often tempting and even successful: the erection of a third taxon of equal level. Kreisel puts the Polyporaceae into an order of their own, Polyporales. If one subscribes to Kreisel's general outlook on Basidiomycete evolution and omits a few groups which he inserts in the Polyporales (in my opinion they do not belong there, e.gr. *Crepidotus*), the order Polyporales (or better a suborder) in this sense might perhaps be acceptable for those, but only for those, who have elevated some Agaricales families to the rank of orders.

I have, as well as Kreisel, originally (1962) included the genus *Schizophyllum* in the Polyporaceae in spite of the absence of any intermediate links between them and the Lentineae and Polyporeae. Donk (1964) has made a good case in favor or recognizing *Schizophyllum* as the type genus of a separate family, including it, together with such genera as *Stromatoscypha* and *Henningsiomycetes* in the Aphyllophorales. The genus *Schizophyllum* differs from other lamellate Basidiomycetes in the tough radial lamellae which split longitudinally, whereby the end-cells of the hyphae of the hymenophoral trama are often cystidiod - abhymenial hairs.

#### KEY TO THE TRIBES

A. Hymenophore neither lamellate nor radially venose, but tubular or absent.

Tribus *Polyporeae*, p. 167

A. Hymenophore lamellate or radially venose

Tribus *Lentineae*, p. 172

Tribus *Polyporeae* (autonym)

*Type genus: Polyporus* Micheli ex Fr.

*Characters:* Those of the family; hymenophore tubulose (or absent).

## KEY TO THE GENERA

- A. Hymenophore well differentiated
- B. Pileus remarkably thin-fleshy (context up to 1 mm thick); pigment present; rameose-lacerate setae absent; hymenophore of tubes with regularly hexagonal pores, the tubes not much longer than the width of the pores, pores forming a concave hymenophoral surface; pseudostipe very short, lateral or resupinately attached, disc-like and often compressed.      2. *Pseudofavolus*, p. 171
- B. Pileus not as above, or hymenophore not as above; pigment present or absent; rameose-lacerate setae present or absent. Stipe often present      1. *Polyporus*, p. 168
- A. Hymenophore none; hymenal surface smooth, with hymenial pegs. Otherwise like *Pseudofavolus*      3. *Mycobonia*, p. 171

### 1. POLYPORUS Micheli ex Fr.

*Syst. Mycol.* 1: 341. 1821.

*Type species:* *P. tuberaster* (Jacq. ex Fr.).

*Syn:* *Favolus* P. Beauv. ex Fr., *Syst. orb. veg.* p. 76. 1825; Fr., *Elench.* 1: 44. 1828.

*Polyporellus* Karst., *Medd. Soc. Fauna Flora Fenn.* 5: 37. 1879.

*Bresadolia* Speg., *An. Soc. Cient. Arg.* 16: 277. 1883.

*Leucoporus* Quél., *Enchiridion* p. 165. 1886.

*Cerioporus* Quél., *l.c.* p. 167.

*Melanopus* Pat., *Hym. d' Eur.* p. 127. 1887.

*Asterochaete* (Pat.) Bond. & Sing., *Ann. Mycol.* 39: 58. 1941.

*Echinochaete* Reid, *Kew Bull.* 17: 283. 1963.

?*Hexagona* Pollini ex Fr., *Fl. scan.* p. 339. 1835\*

*Characters:* Carpophores pleurotoid or with central stipe, true stipe often strongly reduced and pileus almost directly laterally attached; stipe solid, often with fulvous fuliginous to dead black base; if sessile, carpophores with clearly circumscribed disc-like base; sterile surface often fibrillose, squamose, pilose, or radially lineate-striate, margin acute, at times fimbriate-ciliate, pileus hygrophanous or not, its cuticle not separable; tubes with thin walls, rarely tending to be lamellately radiating, but often radially elongated rather than isodiametric in perpendicular section, varying from small to very wide, and then often alveolar, with round to angular pores; context fleshy-toughish to quite tough and in dry condition even almost woody or spongy, rarely pigmented. Spores mostly cylindric or cylindric-ellipsoid-oblong, more rarely ellipsoid-oblong or fusiform, hyaline, sometimes slightly allantoid- curved, smooth, thin-walled, inamyloid; basidia relatively moderately broad, clavate, without carminophilous granulation, almost constantly 4-spored; hyphae more or less hyaline, many of them conspicuously thick-walled, inamyloid, in the cortical layer of the stipe sometimes amyloid, hyphal system monomitic, dimitic, or amphimitic, with clamp connections; cystidia mostly absent or inconspicuous, more rarely present, and then mostly in form of ± rameose-lacerate setae; hymenial pegs often conspicuous. Mycelium with clamp connections, sometimes sclerotia or pseudosclerotia are formed by it. Generally on dead or living

\*The question mark refers to the doubtfulness of the type species of the genus. If *H. mori* (Pollini ex Fr.) Fr. is the type, the genus is synonymous.

wood, rarely on grass (and other herbaceous) roots or seemingly on soil but growing from buried wood.

*Development of the carpophores:* Probably all (certainly gymnocarpous in *P. brumalis*) gymnocarpous; stipitocarpous in the stipitate forms. Under certain conditions coraloid-clavarioid forms develop.

*Area:* Almost cosmopolitan (with the exception of regions without trees; Arctic and Antarctica).

*Limits:* There is no difficulty in delimitation. The only difficulty is the problem whether or not *Polyporus* in the sense and delimitation as it is presented here should be divided into several autonomous genera aside from *Polyporus sensu strictissimo* (the *Polyporus-tuberaster*-group). The best claim for generic distinction has *Favolus* as well as *Asterochaete*, both recognized as subgenera in the present treatment. The rest of the species is by no means fully homogeneous. It is quite possible that *Melanoporus* has claim to generic status and, likewise, proposed by Pouzar as a subgenus (1966), *Leucoporus* Quél. might eventually be separated from *Polyporus*. I maintain subgeneric status for those taxa that can now be circumscribed with precision and postpone the recognition of *Melanoporus* and *Leucoporus* until such time as sufficient data on the anatomy of the hymenophoral trama and the subhymenium as well as on the tramal structure (presence of skeletal and ligative hyphae) will make it possible to arrive at a more precise delimitation of these groups with a well-founded distribution of type species among them. For the time being it is prudent to confine the species list of subgenus *Polyporus* to an alphabetical enumeration of all those Polypori foreign to subgenus *Favolus* and subgenus *Asterochaete*.

A separate problem are the species *Polyporus hirtus* and *P. umbellatus*. Both differ from the rest of *Polyporus*, as demonstrated by Nobles (1971), in that the hyphae of the mycelium in culture remain thin-walled and undifferentiated. Since this may also be the case in some species enumerated here under *Polyporus* subgenus *Polyporus*, I am not fully convinced that *P. hirtus* and *P. umbellatus* should be separated from *Polyporus*, and if so, which other species should be excluded with them.

It is up to the "polyporists" to find eventually a solution for these problems and possibly to investigate the extent of the similarity between certain Hydnoms and *Polyporus hirtus* alluded to by Harrison (1971). The subgenus *Dendropolyoporus* Pouzar (1966) is certainly a necessity. It is based on *Polyporus umbellatus* (Pers. ex Fr. which is not congeneric with *Grifola* nor does it belong in the family Scutigeraceae.

*State of knowledge:* From the preceding paragraphs it may be concluded that the present knowledge of the genus, particularly in relation to modern methods of investigation, is still not very satisfactory. 45 species are here included.

*Practical importance:* Some species of subg. I and II are eaten by South American Indians and most species are wood destroyers, some even weakly parasitic on trees (e.g. *P. squamosus*). *P. tunetanus* and *P. tuberaster* are excellent edible fungi.

## SPECIES

Subgenus I. **Polyporus**. Setae none. Species with favoloid or tubulose hymenophore and corresponding to either *Lentinus* or *Panus* in their hyphal systems and hymenoporal anatomy. Probably a heterogenous group.

Type species: *P. tuberaster* (Jacq. ex) Fr.

*P. admirabilis* Peck; *P. mori* Fr. (*P. alveolaris* D.C. ex Fr.; *Favolus europaeus* Fr.; *F. ohiensis* B. & Mont.; *Favolus canadensis* Klotzsch); *P. arcularius* (Batch ex) Fr. (*P. alveolarius* Bosc.; *P. intermedius* Sing.); *P. badius* (Pers. ex Gray) Schw. (*P. picipes* Fr.); *P. brumalis* (Pers. ex) Fr. [*Polyporus polyporus* (Retz ex) Murr.]; *P. cabocli* Souza & Araujo; *P. ciliatus* Fr. ex Fr.; *P. coronatus* Rostk.; *P. cowellii* Murr. (if different from *P. tricholoma*); *P. craterellus* Berk. & Curt.; *P. dictyopus* Mont.; *P. discoideus* Berk. & Curt. (*P. lenzitoides* Berk.; *P. glutinifer* Berk.; *P. aquosus* Henn.; *P. fuscomaculatus* Bres. & Pat.; *Bresadolia paradoxa* Speg.); *P. gayanus* Lév.; *P. gramocephalus* Berk. (*Favolus*, *Imazeki*); *P. guyanensis* Mont.; *P. handelii* Lohwag; *P. hirtus* Quél. (*P. hispidellus* Peck); *P. infernalis* Berk.; *P. intestinalis* Berk.; *P. kaernbachii* (Henn.) Sing. (*Favolus*, *Henn.*); *P. lentus* Berk.; *P. leprieurii* Mont. and its variety var. *juruuanus* Henn.; *P. maculatissimus* Lloyd; *P. magnivarius* Lloyd; *P. maxonii* (Murr.) Sing. (*Ceriomyces*, *Murr.*); *P. melanopus* (Sw. ex) Fr.; *P. moluccensis* (Mont.) Sing. (*Favolus*, *Mont.*; *F. fibrillosus* Lév.); *P. radicatus* Schw. (*P. morganii* Peck); *P. rhizophilus* (Pat.) Sacc.; *P. sapurema* Moeller; *P. similis* Berk. & Curt.; *P. subradicatus* (Murr.) Sing. (*Scutiger*, *Murr.*); *P. squamosus* (Huds. ex) Fr.; *P. stipitarius* Berk. & Curt.; *P. tricholoma* Mont.; *P. tuberaster* (Jacq. ex) Fr.; *P. tunetanus* (Pat.) Sacc.; *P. varius* (Pers. ex) Fr.; according to Kotlaba also *P. umbellatus* (Pers. ex) Fr. (but will enter a special subgenus).

Subgenus II. (*Favolus* Fr. 1828 non *Polyporus* subgenus *Favolus* (Beauv. ex Fr. 1821). - Setae none. Hymenophore favoloid (with wide radially elongated angular pores); anatomy as in *Pleurotus* sect. *Lentodiellum*; spore print white, cream or pale lilac. Pigments absent, livid, or ochre. Tramal structure amphimitic.

Type species: *Merulius daedaleus* Link = *P. dermoporus* Pers.\*.

*P. dermoporus* Pers. (*Favolus brasiliensis* (Fr.) Fr.); *P. caespitosissimus* Sing. (*P. caespitosus* Lloyd non al.; *Favolus giganteus* Mont.); *P. caperatus* (Murr.) Sing. (*Hexagona*, *Murr.*; *Hexagona reniformis* Murr.); also here: *Hexagona subpurpurascens* Murr. and *P. philippinensis* Berk.

Subgenus III. *Asterochaete* (Pat.) Sing. With more or less colored mostly branched or lacerate setae.

Type species: *P. megaloporus* Mont.

\*A new subgeneric name is not proposed since the status of this group as a subgenus is not final. As a genus it should be called *Favolus* Fr. (with the type species as above but as epitheton of *Favolus* it must be *F. brasiliensis* (Fr.) Fr.). *Favolus* as a subgenus of *Polyporus* is preoccupied by *Polyporus* subgen. *Favolus* (Beauv. ex) Fr. 1821 with a type species (*Favolus hirtus* Beauv.) belonging to another group: *Hexagonia* = *Scenidium* (Aphyllophorales).

*P. cinnamomeosquamulosus* Henn. (Asterochaete, Bond. & Sing.; Echinochaete, Reid); *P. coracinus* Murr. (Asterochaete, Bond. & Sing.; *P. princeps* Sing. (P. megaloporus Mont. non Pers.; Echinochaete, Reid; ?*Favolus princeps* Berk. & Curt.); *P. russiceps* Berk. & Br. (Asterochaete Bond. & Sing.; Echinochaete, Reid).

## 2. PSEUDOFAVOLUS Pat.

*Essai taxon.* p. 80. 1900.

*Type species:* *Pseudofavolus cucullatus* (Mont.) Pat.

*Characters:* Those of the key. Otherwise those of the family.

*Development of the carpophores:* Unknown.

*Area:* Neotropical and subtropical.

*Limits:* The genus is closest to subgenus II of *Polyporus* from which it is easily separated. Although the slightly gelatinized subhymenium is well developed as in *Pleurotus*, there is never a tendency to form lamellae. Externally, the carpophores of *Pseudofavolus* are so similar to those of *Mycobonia* that it is difficult to distinguish the former from the latter unless the hymenophore is seen.

*State of knowledge:* Only two species are known to this author.

*Practical importance:* Unknown.

## SPECIES

*P. cucullatus* (Mont.) Pat.; *P. auriculatus* Pat.

### Reduced series: 3. MYCOBONIA Pat.

*Bull. Soc. Mycol. Fr.* 10: 76. 1894, *nomen conservandum*.

*Type species:* *Hydnum flavum* (Sw. ex Fr.) Berk.

*Syn:* *Hirneola* Fr., *Syst. Orb. Veg.* p. 93. 1825, *non* Fr. 1848 *nec* Velen. (1939)  
*Grandinioides* Bunker, *Mem. Torr. Bot. Cl.* 12: 179. 1906.

*Characters:* Habit exactly as in *Pseudofavolus*, but spores larger (13.5-22 × (4.5)-7-11 µm), and hymenophore lacking even in age. Basidia mostly 4-spored, rarely (1)-2-(4)-spored, 31-55 µm long; basidioles elongate-claviform. True cystidia none but numerous hymenial hyphae breaking through the basidial layer and inserting themselves between the basidia, thick-walled, subacute or acute, 2 µm in diameter, often combined into pegs which consist of more or less interwoven hyphae of the same kind but in age and in dried material more pigmented (pegs in KOH varying from honey yellow to chestnut) and otherwise much like the pegs of *Heterochaete*, very conspicuous and macroscopically showing as dark (fresh white to purple)

colored "setae", numerous and conspicuous under a hand lens, otherwise hymenium smooth; subhymenium scarcely differentiated; hyphae of the context hyaline, here also some larger generative and strongly elongated and thick-walled but often rameous (skeletals?) hyphae and numerous thin-walled "connecting" hyphae; clamp connections present. External layer of the pileus dense, consisting of interwoven thick-walled pigmented hyphae, otherwise not differentiated. No amyloid or pseudoamyloid elements in the trama of the pileus. On dead wood.

*Development of the carpophores:* Primordia not studied. The very young (2 mm) carpophore shows involute margin and is entirely ochraceous yellow.

*Area:* American tropics and subtropics.

*Limits:* The absence of a hymenophore differentiates the genus clearly from other Polyporaceae. However, this genus is not, as may otherwise be expected, related to any "hydnaceous" or "stereaceous" genus.

My insertion of *Mycobonia* in the Polyporaceae (1951) has evoked two comments which I quote here together:

"I think by including *Mycobonia* in the Polyporaceae [Singer] has deemphasized the taxonomic value of the configuration of the hymenophore to an almost ridiculous degree", A.H. Smith (*Mycologia* 55: 696. 1963).

"[*Mycobonia*] closely related to *Pseudofavolus* Pat. (Polyporaceae)", M.A. Donk, *Persoonia* 3: 294. 1964.

*State of knowledge:* Only one species is known (cf. Martin, *Mycologia* 31: 247-249. 1939).

*Practical importance:* Unknown.

## SPECIES

*M. flava* (Sw. ex Fr.) Pat.

### Tribus *Lentineae* Fayod

*Prodr. Am. Sci. Nat. Bot.* VII, 9: 335. 1889 (ut Agaricinées tribu *Lentinés*); Ulbrich, *Höh. Pilze*, p. 212. 1928. Heim, *Treb. Mus. Cienc. Nat. Barcelona* 15: 88. 1934; Imai, *Journ. Fac. Agaric. Hokk. Imp. Univ.* 93: 141. 1938.

*Type genus:* *Lentinus* Fr.

*Syn.:* Agaricacés trib. *Pleurotés*, Kühner, Contrib. p. 98.  
*Nothopaneae* Kühn., *Bull. Soc. Linn. Lyon* 49: 233. 1980.

*Characters:* Those of the subfamily but hymenophore always present at first sometimes venose but at full maturity truly lamellar, except in *Geopetalum* where it remains venose.

## KEY TO THE GENERA

- A. Lamellae deep colored, especially in dried material but also in fresh condition; black carbonaceous particles often present in the tissues; pigment dissolving in alkali forming a greenish solution.  
(See *Anthracophyllum*, p. 312)
- A. Hymenophore not deep colored in fresh condition, and hardly ever deep colored in well dried material; carbonaceous particles absent, tissue never green in alkali.
- B. Stipe absent and veil present; hymenophore lamellate; spore print whitish; spores small (3-5.5 × 1-1.7 µm).  
(See *Tectella*, p. 347)
- B. Not combining the characters indicated above.
- C. Spores large, cream in print; a pellicular veil present (stipe none).  
(See *Pleurotus*, p. 174)
- C. Not combining these characters indicated above.
- D. Hymenophore chambered irregularly.  
(See *Lentodium*, p. 180)
- D. Hymenophore lamellate or venose.
- E. Spore print distinctly pink when fresh (salmon pink), bleaching to white by dehydration (in the herbarium); spores small, mostly allantoid; pileus with a hygrophanous tomentum; hyphal system monomitic with sclerified hyphae.  
4. *Phyllotopsis*, p. 173
- E. Spore print white, cream, pale livid-lilac, more rarely pink; spores allantoid or cylindric; hyphal system monomitic, dimitic or amphimitic; if the spore print is pink, the pileus is glabrous.
- F. Hymenophoral trama irregular; subhymenium very inconspicuous, almost absent; hymenophore lamellate and more or less decurrent, with entire edge; hyphal system not monomitic; pileus and/or stipe often strongly pilose or dotted; stipe mostly well developed  
6. *Panus*, p. 179
- F. Either the hymenophoral trama is regular or the subhymenium is strongly developed, or both.
- G. Hymenophore lamellate, or if initially venose, without metuloids.
- H. Hymenophoral trama irregular; subhymenium well developed; (in some veiled species, the hymenophore hyphae at times remaining subregular and thin-walled for a long time); in monomitic species spore print mostly colored cream, or most frequently pale livid-lilac or livid-pallid, rarely pure white; metuloids present only in amphimitic groups. Lamellae mostly entire.  
5. *Pleurotus*, p. 174
- H. Hymenophoral trama regular at least towards the edges of the lamellae and always quite regular in veiled forms; subhymenium well developed or almost absent. Hyphal system monomitic or dimitic, not amphimitic. Metuloids or conspicuous lamprocystidia often present. Spore print white to cream (Romagnesi Ib) to pure white. Lamellae mostly serrate.  
7. *Lentinus*, p. 183
- G. Hymenophore consisting of radial veins, rarely very narrow lamellae; pseudoamyloid metuloids and endocystidia present.  
8. *Geopetalum*, p. 188

## 4. PHYLLOTOPSIS (Gilbert & Donk apud Pilát) ex Sing.

*Rev. Mycologie* 1: 76. 1936; *Beih. Bot. Centr.* (B) 56: 143. 1936.

*Type species:* *P. nidulans* (Pers. ex Fr.) Sing.

*Syn.:* *Pleurotus*, sect. *Phyllotopsis* Gilbert & Donk in litt., apud Pilát in Kavina & Pilát, *Atlas Champ. Europe*, *Pleurotus* 14-15: 169. 1935 (no Latin).

Pileus covered by a hygrophanous, dense tomentum (the tomentum regaining its color when moistened even in herbarium specimens), non-stipitate, usually lateral; hymenophore lamellae not white; spore print pink, bleaching to white in the

herbarium; spores hyaline, small, cylindric to allantoid, inamyloid, smooth, thin-walled; basidia normal in every regard, 4-spored; cystidia none; if cheilocystidia are present, they are small, inconspicuous, filamentous, hyphae-like; hymenophoral trama regular to subregular, consisting of subparallel to more or less interwoven hyphae with distinct axillar arrangement; subhymenium little differentiated, its elements smaller and shorter than those of the trama but not well separated from the latter; context rather thick, fleshy-tough, monomitic with many ± sclerified hyphae; inamyloid, with numerous septa and clamp connections (Pl. 28). On wood.

*Development of the carpophores:* gymnocarpous.

*Area:* Temperate zones of both hemispheres, in Argentina, Brazil, and South Africa.

*Limits:* This genus is small but well characterized by the color of the spore print, the shape of the spores and their size, the hygrophanous tomentum, the absence of metuloids and a stipe, and monomitic trama.

*State of knowledge:* The type species is thoroughly known.

*Practical importance:* The type species is an active destroyer of wood, growing in hardwood as well as in coniferous wood.

## SPECIES

*P. nidulans* (Pers. ex Fr.) Sing. (*Pleurotus*, Gillet; *Crepidotus*, Quél.; *Panus*, Pilát; *Claudopus*, Karst; *Crepidotus junquilleus* (Paulet ex Lév.) Quél.; *Panus stevensonii* Berk. & Curt.; *Panus domicola* Speg.; *Agaricus odoratus* Britz.); *P. salmonaea* (Kalchbr. & MacOwan) Reid.

### 5. PLEUROTUS (Fr.) Quél.

*Champ. Jura Vosg. p. 62. 1872 em., nomen conservandum.*

*Type species:* *P. ostreatus* (Jacq. et Fr.) Kummer.

Syn.: *Agaricus* trib. *Pleurotus* Fr., *Syst. Mycol.* 1: 178. 1821.

*Crepidopus* Nees ex S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 616. 1821 (proposed for rejection).

*Cyclopleuropus* Van Hasselt, *Alg. Konst en Letter-Bode* 15: (231). 1824 (not validly published) (type: "Merulius Cyclopleuropus..." = *P. dactyliophorus* Lév.-L.).

*Pleurotus* Kummer, *Führ. Pilzk.* p. 24. 1871 (homon. & synon.).

*Pleurotus* Quél., *Enchir.*, p. 147. 1886 (homon. & synon.).

*Dendrosarcus* Paulet ex Kunze, *Rev. Gen. Pl.* 2: 462. 1889 nom. nud.

*Antromycopsis* Pat. & Trabut, *Bull. Soc. Myc. Fr.* 13: 215. 1897 (imperfect form of sect. *Coremio-pleurotus* (see Pollack & Miller, *Mem. N.Y. Bot. Gard.* 28: 174-178. 1976)).

*Lentodiopsis* Bubák, *Hedwigia* 43: 169. 1904 (type *L. albida* Bubák, l.c.).

*Lentodiellum* Murr., *Mycologia* 7: 216. 1915 (type *Panus concavus* Berk.).

*Nothopanus* Sing., *Mycologia* 36: 364. 1944.

?*Pterophyllus* Lév., *Ann. Sc. Nat.* III. 2: 178. 1844 (type *P. bovei* Lév.).

**Characters:** Habit pleurotoid; pigment absent or almost absent, or present, and then grayish to fuscous-umber, more rarely blue, green, red, yellow or lilac; hymenophore lamellate; hymenophoral trama initially often  $\pm$  regular, becoming completely irregular, consisting of thin-walled or thick-walled hyphae (in the first case, veil present, and metuloids absent; in the second case, veil present or absent, metuloids present or absent); spore print pure white, or cream color, or very frequently pale drab 43-B-2 or "opal, mauve" M. & P. ("tilleul buff", or paler - according to Ridgway's chart, or somewhat paler than "pale vinaceous buff"), rarely pink; spores hyaline, smooth, always cylindric, from rather small to large, with very thin to rather thin, simple, inamyloid walls; basidia normal in every regard; metuloids often present; cheilocystidia usually present; subhymenium (Pl. 27, 4) always strongly developed, well differentiated and broad ( $>7 \mu\text{m}$  deep) differing from the irregular hymenophoral trama in the small size of the elements and often also in color (in dried material pale brownish instead of hyaline), often actually separating from the hymenophoral trama in alkaline media under slight pressure; stipe present, more rarely absent, at least as seen from above, and then the carpophores sessile; context fleshy to moderately tough and somewhat inclined to revive after remoistening; trama of the pileus inamyloid, its hyphae with numerous clamp connections. Hyphal system mono-, di-, or amphimitic. A coremial asexual state, often formed in synnematoid fructifications present in one section. On wood, more rarely on other plant tissues, on dead and on living hosts, very rarely on bones, or on the earth (probably seemingly so, actually on buried vegetable matter), mycelium often nematophagous.

**Development of the carpophores:** Metavelangiocarpous (*P. dryinus*) or gymnocarpous to slightly stipitangiocarpous in *Pleurotus ostreatus* according to Reijnders. Some species are definitely angiocarpous as has been suspected by Kühner. Light deficiency provokes coraloid forms in several species.

**Area:** Cosmopolitan.

**Limits:** The traditional genera of this group, *Pleurotus*, *Lentinus*, and *Panus*, have been shown to be artificial in their classical limits. During the last decades, several mycologists have contributed to their dismemberment, leaving a comparatively small nucleus of species within each of the old genera. However, the delimitation of the three genera from each other and the choice of nomenclatory type in each of the various generic taxa has been anything but unanimous.

Two approaches were possible, both anatomical: either the presence or absence of metuloids could be made the major distinguishing character between *Panus* and *Pleurotus*, with *Lentinus* maintained according to the traditional macroscopical differences; or the structure of the sterile tissues of the hymenophore could be used for generic delimitation. After checking on all the key species, and a large number of additional types, the author has decided in favor of the second principle. The metuloids do not seem to be quite constant. In some species of the section *Lentodiellum* which has been scattered among the *Pleuroti*, *Pani*, and *Lentini* by the authors of the past century, the species with metuloids pass almost imperceptively into species without them and these again are too close to the

*Ostreatus*-group of *Pleurotus* to be separated from it generically. All these species have two characters in common: the irregular hymenophoral trama and the distinct subhymenium. The genus *Panus* is then separated on the basis of the virtual absence of the subhymenium (or a very reduced, inconspicuous subhymenium <5(-8) µm deep may be present). In this case, we shall again find species with metuloids and without metuloids in the same genus, even in the same section. Consequently what is left in the genus *Lentinus*, i.e. the groups *L. lepideus*, *L. adhaerens*, etc. can be separated from both *Panus* and *Pleurotus* by their subregular to regular hymenophoral trama. In *Panus* and *Lentinus*, we find metuloids (in the latter more elongate and less thick-walled) in some species while they are absent in the majority of the species. It appears, therefore, that the metuloids must be considered as a potential character in the *Lentineae*, or rather in the group *Pleurotus-Panus-Lentinus*, but not as a generic character. When the species belonging to these three genera are sorted out according to their anatomical characters of the sterile tissues of the hymenophore, one will find that they are distributed along natural lines - each of the three emended genera now being perfectly homogeneous taxonomic groups, and the mycologist interested in the determination of the species is no longer compelled to go through all three genera in order to avoid missing the description of the species he is studying.

A study of the hyphal systems (see also Ľ. Stankovičová 1973) of the *Lentineae* shows that mono-, di- and amphimitic structures are found in certain genera (*Pleurotus*), only di- and amphimitic in *Panus*, only mono- and dimitic in *Lentinus*, only monomitic in *Phyllotopsis*, and only dimitic in *Geopetalum*. On the other hand, the hyphal systems appear to be fairly constant in the existing sections, and the obvious conclusion is that hyphal systems in the Polyporaceae are not necessarily generic characters, but are useful as sectional characters. An analysis of the pigments would probably lead to a similar conclusion. In section *Lentodiellum* of *Pleurotus*, the absence or scarcity of pigments on the pileus appears to be useful for the delimitation against *Panus*. And in *Panus* the occurrence of non-persisting violet-lilac pigments (in both sections) is worthy of further chemical investigation since these pigments have not been observed in other genera of the *Lentineae*.

As for the separation of *Pleurotus* from *Panus* and *Lentinus*, see under those genera.

*State of knowledge:* A modern world monograph of *Pleurotus* is still missing, but Hilber (1982) has published an excellent book mainly on European species with inclusion of a few American and Asiatic taxa. This work, containing the badly needed crossing experiments of monospore cultures, may be used as an example how to proceed further and is therefore a valuable basis for *Pleurotus* studies. Hilber did not include sect. *Lentodiellum* (following "vorläufig" Pegler and Corner) but thinks that subgen. *Coremiopleurotus* (here section) represents a transition to sect. *Lentodiellum*. Since the transfer of sect. *Lentodiellum* to *Lentinus* is not acceptable because of nomenclatorial reasons, the question is clearly reduced to a choice between insertion of sect. *Lentodiellum* in *Panus* or *Pleurotus* (with regard to this I refer to our discussions on *Panus* and *Lentinus*). Since I see no

reason to abandon sect. *Lentodiellum* within *Pleurotus*, the number of well known species, studied by me personally, is now 38.

**Practical importance:** The sclerotium of *P. tuberregium* serves the natives for medicinal purposes. All species are edible, especially those of sect. 3 and 4 but also *P. sajorcaju*. *P. ostreatus* and related species and *P. abalonus* are commercially cultivated.

## SPECIES

Sect. 1. LEPIOTARII (Fr.) Pilát in Kaviná & Pilát (1935) (genus *Lentodiopsis* Bubák; subgenus *Lentodiopsis* (Bubák) Hilber 1981). With a distinct veil and a distinct stipe. Synnematoid fructifications absent. Hyphal system in mature carpophores dimitic (in two species unknown).

*Type species:* *P. dryinus* (Pers. ex Fr.) Kummer

*P. dryinus* (Pers. ex Fr.) Kummer [*Armillaria*, Schroeter; *Armillariella* Pat.; *Pleurotus corticatus* (Fr. ex Fr.) Quél.; *P. pometi* (Fr.) Quél.] with var. *tephrotrichus* (Fr. ex Secr.) Gill. [*Pleurotus albertinii* (Fr.) Quél.; *Lentodiopsis albida* Bubák]; *P. rickii* Bres., and *P. lindquistii* Sing.

Sect. 2. CALYPTRATI Sing. (1962). Pileus with a pellicular veil; stipe strongly reduced; trama of the lamellae irregular, many hyphae thick-walled, dimitic with unbranched skeletals (Stankvicčvá), with many arboriform (ligative?) ones (Hilber).

*Type and only species:* *P. calypratus* (Lindb. in Fr.) Sacc. (*Agaricus*, Fr.; *Tectella*, Sing. 1943).

Sect. 3. PLEUROTUS. Without a distinct veil but often with a distinct stipe. Synnematoid fructifications absent. Hyphal system in mature carpophores monomitic or dimitic (in several species unknown). Spore print color white to ivory or pale livid-violet, often whitish then pale livid violet or pale livid, rarely pink.

*Type species:* *P. ostreatus* (Jacqu. ex Fr.) Kummer

1. Species with monomitic hyphal system:

*P. ostreatus* (Jacqu. ex Fr.) Kummer (with var. *ostreatus* and var. *columbinus* (Quél. apud Bres.) Quél.; *P. pulmonarius* (Fr.) Quél.; *P. citrinopileatus* Sing.; *P. flabellatus* (Berk. & Br.) Sacc.; *P. eugrammus* (Mont.) Dennis; *P. eryngii* (D.C. ex Fr.) Quél.; *P. subsapidus* (Murr.) Murr.

2. Species with dimitic hyphal system:

*P. ostreatoroseus* Sing.; *P. opuntiae* (Dur. & Lév.) Sacc.; *P. macropus* Bagl.\*

3. Hyphal system unknown:

*P. laciniatocrenatus* (Speg.) Speg.; *P. euosmus* (Berk. apud Hussey) Sacc.; *P.*

\**P. cornucopiae* (Paulet ex Fr.) Rolland sensu Kühn. & Rom., Hilber vix Paulet, Fr.

*phellogenae* Sing.; *P. araucariicola* Sing.; *P. pantoleucus* (Fr.) Gillet; *P. prometheus* (Berk. & Curt.) Sacc.; probably also *P. yuccae* Maire; *P. convivaram* Dunal & Delille apud Lagarde; *P. parthenopeius* (Comes) Sacc.; *P. salignus* (Pers. ex Fr.) Kummer (but these four especially the latter may be conspecific with *P. ostreatus*); also *P. importatus* Henn. and *P. gemmelari* (Inz.) Sacc. - *P. lobulatus* (Lév.) Sacc. is probably an older name for *P. flabellatus*.

Sect. 4. COREMIOPLEUROTUS (Hilber) st. n. (subgen. *Cōremiopleurotus* Hilber, Gatt. Pleurotus p. 215, 1982). Without a distinct veil, with ramified or entire and then eccentric or lateral stipe. Synnematoid fructifications and chlamydospores similar to those formed in these fructifications present. Hyphal system monomitic. Spore print white or pale, cream, never livid or pink. Cheilocystidia and dermatocystidia strongly developed.

Type species: *Pleurotus cystidiosus* O.K. Miller

*P. cystidiosus* Miller; *P. abalonus* Han, Chen & Cheng (the latter probably a geographical race of the former)

Sect. 5. LENTODIELLUM (Murr.) Sing. (genus *Lentodiellum* Murr.). Without or with a distinct veil, if veiled either finely strigose and white (tending to yellowing) or with amphimitic hyphal system. Hyphal system never monomitic, mostly amphimitic, with skeleto-binding hyphae, or dimitic. With or without a distinct stipe. Synnematoid fructifications not observed. Spore print white to cream color, not livid nor pink. Pileus and stipe basically white, but sometimes with a flush of cinnamon, brown, buff or ferruginous. Pachyma-sclerotia none, but stipe sometimes branching from a common base (pl. 57, below).

Type species: *Panus concavus* Berk.

#### 1. Species without metuloids:

*P. levis* (Berk. & Curt.) Sing. (*Panus*, B. & C.); *P. strigosus* (Berk. & Curt.) Sing. (unless too close to the first species); *P. hirtus* (Fr.) Sing. (*Agaricus* Fr. non Secr. nec Wallr.; *Panus*, Fr.); *P. concavus* (Berk.) Sing. (*Panus*, Berk.; *Lentodiellum*, Murr.; *Clitocybe* *augustinensis* Sing. acc. to Corner); *P. fockei* (Miquel) Sing. (*Lentinus*, Miquel; *L. striatulus* Lév. non *Pleurotus striatulus* (Pers. ex Fr.) Quél.; *L. calvescens* Berk.\*); *P. calyx* (Speg.) Sing. (*Clitocybe*, Speg.); *P. sajorcaju* (Fr.) Sing. (*Agaricus*, Fr.; *Lentinus* Fr.; *L. exilis* Klotzsch ex Fr.; *L. murrayi* Kalchbr. & MacOwan); *P. squarrulosus* (Mont.) Sing. (*Lentinus*, Mont.; *L. subnudus* Berk.; *L. curreyanus* Sacc. & Cub.; *L. manipularis* Berk. & Br.; *L. cretaceus* Berk. & Br.; *L. lobatus* Berk. & Br.; *L. multiformis* Berk. & Br.; *L. inconspicuus* Berk.; *L. bavianus* Pat.). - *P. dactyliophorus* (Lév. as *Lentinus*) and *P. leucochrous* (Lév. as *Lentinus*) also belong in this section but may be conspecific with *P. sajorcaju* or *P. squarrulosus* respectively.

#### 2. Species with numerous distinct metuloids

\*erroneously quoted as *Panus calvescens* Berk. by Corner (1981).

Sect. 6. *TUBERREGIUM* Sing. (1961). Somewhat more pigmented on the pileus than in sect. 5; veil slight; stipe distinct eccentric to more often  $\pm$  central. Synnematoid fructifications none. Hyphal system dimitic with skeletals. Rising from a conspicuous Pachyma-sclerotium.

Type species: *P. tuberregium* (Fr.) Sing.

*P. tuberregium* (Fr.) Sing. (Lentinus, (Fr.) Fr.; Panus, Corner; Lentinus baguirmensis Pat. & Har.; Lentinus woermannii Cohn & Henn.)

## 6. PANUS Fr.

*Epicrisis*, p. 396. 1838, em.\*, nom conserv. with:

Type species: *P. conchatus* (Bull. ex Fr.) Fr.

Syn.: *Pleurotus* (Pers. ex) S.F. Gray, *Nat. arr. Brit. Pl.* 1: 615. 1821 (type: *A. fornicate* Pers.).

*Scleroma* Fr., *Epicr.*, p. 387. 1838 (lectotype: *Lentinus velutinus* Fr.).

*Pocillaria* B. Browne ex O. Kuntze, *Rev. Gen. Pl.* 2: 865. 1891.

*Lentinopanus* (Pilát ut sect. *Pleuroti*) Pilát, *Ann. Mycol.* 39: 73. 1941 [1942].

*Lentodium* Morgan, *Journ. Cincinnati Soc. Nat. Hist.* 18: 36. 1895.

**Characters:** Habit pleurotoid, but often with central stipe, and then differing from the genera with non-pleurotoid habit in being very tough and reviving, and growing on wood; pigment present but usually not bright colored except in fresh specimens of some species where it is lilac; hymenophore lamellate; lamellae decurrent (if there is a stipe); hymenophoral trama completely irregular, (Pl. 24, 1) in age, rarely distinctly and persistently bilateral, consisting of thick-walled hyphae; spore print white; spores hyaline, smooth, inamyloid, always cylindric, from rather small to medium (mostly not more than 8  $\mu\text{m}$  long), with very thin to rather thin simple wall; basidia normal in every regard; metuloids often present, and then usually obtuse at the apex and rather short, with extremely thick walls, mostly moderately numerous; hyphal pegs sometimes present in the hymenium; subhymenium very narrow (up to 5-7  $\mu\text{m}$  deep) or little developed (Pl. 24, 1) edge of the lamellae lacerate-denticulate-

\*The genus *Panus* has been conserved with the type species, *P. conchatus*. Thus, those who use *P. stypticus*, the type of *Panellus*, as the type of *Panus* are obviously violating the rules of the Code. There is no reason why this should be changed by reconsideration of the Congress since Fries cites in the protologue "Lentini Secr. in Indice" as synonym. This list of species (*Secretan* 3: 54. 1833) contains *A. conchatus*, not *A. stypticus* nor any *Panellus*. Besides, "St. P. stiptici. Pani genuini." means the same as it means in other cases, namely that the stirps contains species which are genuine Pani in Fries's concept. It does not mean that a stirps of *P. stypticus* are selected as nomenclatorial type species in the sense that this stirps is more genuinely a *Panus* than any other.

Kühner (1980) who generally is in agreement with the taxonomy and nomenclature used in the present work, has nevertheless preferred a wider genus concept combining, for example, *Panus* and *Pleurotus* into a single genus. For those who, like him, prefer larger genera, it is however necessary to remember that *Panus* cannot be considered to be a subgenus of *Pleurotus*, and if in this case the rules of the Code are applied, all species of *Pleurotus* would have to be transferred to *Panus*.

crenulate, or entire; stipe present, more rarely absent and then carpophores sessile; veil usually none; context very tough and reviving on remoistening, di- or i.e. trama consisting of generative and skeletal or skeletal-binding hyphae; clamp connections numerous. On wood.

*Development of the carpophores:* Gymnocalypous in *Panus conchatus* and *P. suavissimus* (Reijnders, Kühner), probably almost (secondarily?) angiocarpous in some hairy species where part of the hymenia of the primordia is hidden under the involute margin; mix-angiocarpous in *P. tigrinus*

*Area:* Pantropical and cosmopolitan species predominant.

*Limits:* The delimitation of this genus against *Pleurotus* and *Lentinus* is evident from the key to the genera (p. 173). The predominantly white species with finely short- and soft pilose-velutinous pilei and (often) a tendency to yellowing are even macroscopically recognizable as belonging to *Pleurotus*; they have a concipuous subhymenium and sometimes a conspicuous veil. The species with coarsely hirsute or hairy pileus, only rarely almost pigment-less, without a distinct floccose or annular veil, but often with a lilac or purplish violet tinge when fresh, are easily recognized as belonging to *Panus*. Those with pseudosclerotium are likely to belong to *Panus*, those with Pachyma-sclerotium - to *Pleurotus*. As for *Lentinus*, the structure of the lamellar trama - irregular, rarely bilateral, in mature specimens of *Panus*, always regular or subregular in corresponding specimens of *Lentinus* - provide a sharp hiatus between the two genera.

In some species of *Lentinus* there is an intermixed mediostratum between a regular lateral stratum or hymenopodium. This is discussed under *Lentinus* (p. 184).

Morgan and Murrill recognize *Lentodium* as a separate genus, with *L. squamulosum* as type species. This species is, however, obviously the product of a gasteromycetation process (see chapter V.). It is therefore homologous to the similar *Lentinus edodes* f. *sterilis*, and all characters of this fungus are identical with those of *Panus tigrinus* with the exception of the hymenophore. I have now studied several fertile specimens of the *Lentodium*-form of *P. tigrinus*. M.A. Rosinsky & A.D. Robinson (*Amer. J. Bot.* 55: 242-246. 1968) indicate that crosses between monocaryotic isolates of strains of *Lentodium squamulosum* and one strain of normal *Panus tigrinus* showed complete intercompatibility. These data refute G.W. Martin's (1956) suggestion according to which the *Lentodium*-form of *Panus tigrinus* represents an independent genus and species intermediate between Gasteromycetes and Agaricales like *Galeropsis* etc. It is only regrettable that Rosinsky & Robinson's highly informative work contains a "non-sequitur" of phylogenetic conclusions. A mutation which implies the loss of a geotropic hymenophore and

thus free spore fall, in spite of maintaining the spore projection apparatus of the autobasidium does not produce a gastromycete. Genetic change is occasionally found at some level of a single mycelium (as in "sectoring") since one observes among the carpophores of a single thallus, in some localities, both lamellate and gastroid forms. Moreover, even if one wanted to construct a line from the *Lentodium*-forms to the true Gastromycetes - it would be impossible to find an even vaguely comparable genus or species among the latter.

*State of knowledge:* Our present knowledge of the species of *Panus* is very satisfactory. There are only 13 species definitely accepted here (see Pl. 5; 24, 1).

*Practical importance:* All species are very active wood destroyers. *P. rufus* is important in the preparation of *airan* (a fermented milk product) in the Caucasus.

## SPECIES

Sect. 1. *PLEUROTI* (Sacc. 1887 ut sect. generis *Lentini*) Sing. Metuloids none; pileus glabrous; tramal hyphae rather thin, the majority almost solid or with very narrow lumen; edge of the lamellae denticulate: stipe eccentric, lateral, or absent; if the stipe is present, there is usually a deep red zone at the base corresponding to the black zone of "*Melanopus*" in *Polyporus*; hyphal system amphimitic.

*Type species:* *Lentinus suavissimus* Fr.

*P. suavissimus* (Fr.) Sing. (*Lentinus*, Fr.; *Lentinus haematopus* Berk.; *Panellus*, Murr.; *Lentinus anisatus* Henn.).

*Note:* This section corresponds to *Polyporus guyanensis* and related species.

Sect. 2. *CRINITI* (Sacc.) Sing. (*Lentinus*, sect. *Mesopodes* subsect. *Criniti* Sacc. 1887) *Pleurotus* subgen. *Lentinus* Kühn, *Bull. Soc. Linn. Lyon* 49: 197. 1980. Metuloids few or none; pegs in the hymenium generally present, pileus often pilose or with pilose-fibrous squamules, often striate; hyphae of the hymenophoral trama filamentous, moderately thin, not many almost solid; edge of the lamellae either permanently entire, or becoming lacerate-serrulate or almost denticulate in age; stipe central or eccentric; hyphal system amphimitic.

*Type species:* *Lentinus crinitus* (L. ex Fr.) Fr.

*P. tigrinus* (Bull. ex Fr.) Sing. (*Lentinus*, Fr.); *P. crinitus* (L. ex Fr.) Sing. [*Lentinus*, Fr.; *L. bertieri* (Fr.) Fr.; *L. swartzii* Berk.; *L. schomburgkii* Berk.; *L. stupens* Klotzsch\*; *L. stuppeus* Klotzsch ex Fr.; *L. villosus* Fr. sensu Berk. & Curt.; *L. zeyheri* Berk.; *L. nicotianus* Berk.; *L. crassipes* Berk.; *L. fumigatus* Lév.; *L. wrightii* Berk. & Curt.; *L. subcervinus* Berk. & Curt.; *L. rigidulus* Berk. & Curt.; *L. pyramidatus* Berk. & Curt.; *L. nicaraguensis* Berk. & Curt.] with var. *schnyderi*

\*This is the original spelling, later changed to "stipeus" or "stuppeus" by other authors. It has been considered different by some authors, e.g. Pegler & Rayner (*Kew Bull.* 23: 389. 1969) but its characters are basically the same as in *P. crinitus* which is very variable.

(Speg.) Sing. (*Lentinus schnyderi* Speg.); *P. prancei* (Sing.) Sing. (*Lentinus prancei* Sing. *Nova Hedw.* 35: 152. 1981); *P. badius* (Berk.) Sing.; *P. brevipes* (Cooke) Sing. (*Lentinus*, Cooke); *P. inquinans* (Berk.) Sing. (*Lentinus*, Berk.); *P. polychrous* (Lév.) Sing. (*Lentinus*, Lév.; *L. praerigidus* Berk.; *L. kurzianus* Currey; *L. eximus* Berk. & Br.; *L. thwaitesii* Berk. & Br.; *L. striatus* Berk. & Br.)

Sect. 3. *FULVI* Sing.\*. Differing in dimitic (with skeletals only) hyphal system, exceptional or no hyphal pegs. Pseudosclerotia often formed (pl. 5). Tropical and subtropical species.

Type species: *Panus fulvus* (Berk.) Pegler & Rayner (sensu P. & R.)

*P. fulvus* (Berk.) Pegler & Rayner (sensu Pegler & Rayner, Corner; *Lentinus*, Berk.; *Lentinus velutinus* Fr.; *Panus*, Chardon & Toro, non Fr.; *Panus siparius* (Berk. & Curt.) Sing; *Lentinus*, Berk. & Curt.; *L. leprieurii* Mont., non *Panus leprieurii* Mont.; *Lentinus velutinus* var. *lepraeurii* (Mont.) Dennis; *L. fallax* Speg.; *L. tephroleucus* Mont.; *L. dichrous* Lév. in Zollinger at least sensu Pat., Bres., Lloyd, Pilát; *L. zonatus* Lév.; *L. zonifer* Berk. & Br.; *L. nepalensis* Berl.; *L. egregius* Mass.; *L. fuscopurpureus* Kalchbr.; *L. velutinus* var. *fuscopurpureus* (Kalchbr.) Pilát; *L. fastuosus* Kalchbr. & McOw.; *L. similis* Berk. & Br.]; *P. javanicus* (Lév.) Corner (*Lentinus*, Lév.; *L. revelatus* Berk.; *L. infundibuliformis* Berk. & Br.)

Sect. 4. *PANUS* (Genus *Lentinopanus* Pilát; sect. Conchati Fr. 1868). Obtuse metuloids usually present although sometimes rather scattered, with very thick walls and little (if at all) projecting; pileus hirsute, in the center sometimes squamulose at the same time, or entirely glabrous (but then metuloids quite constant) and smooth; pigment some kind of pale brownish ochraceous, or almost cinnamon, often flushed with a beautiful lilac when quite fresh (not regained when revived); edge of lamellae not denticulate, always entire; hymenophoral trama as in sect. 2; hyphal system dimitic (with skeletals).

Type species: *P. conchatus* (Bull. ex Fr.) Fr.

*P. conchatus* (Bull. ex Fr.) Fr. (*Lentinus*, Schröter) non Mont.; [*P. torulosus* (Pers. ex Fr.) Fr.; *Lentinus carneotomentosus* (Batsch ex) Schröter]; *P. rufus* Fr. [*Pleurotus*, Pilát; *Lentinus strigosus* (Schwein.) Fr. non *Panus strigosus* Berk. & Curt.; *Agaricus hirtus* Secr. non Fr.; *Lentinus lecomtei* Fr. 1828 p.p. ss. aut. amer. non Schweinitz qui *A. crinitus* Schwein. = *P. crinitus* (L. ex Fr.) Sing.; *Panus guaraniticus* Speg.; *Lentinus martianoffianus* Kalchbr.; *Panus sainsonii* (Lév.) Heufler; *Panus semirufus* Sing.; *Lentinus sparsibarbis* Berk. & Curt.; *Lentinus strigellus* Berk. & Curt.; *Panus*, Chardon & Toro], with at least two varieties, one of them common in the tropics and subtropics, var. *strigellus* (Berk. & Curt.) Sing.; *P. fasciatus* (Berk.) Sing. ex Pegler.

\* sect. nov. Systemate hyphali dimitico; metuloideis typicis (sectionis Pani) et fasciculis hyphalibus hymenialibus nullis (sed pleurocystidiis interdum praesentibus). Typus sectionis: *P. fulvus* (Berk.) Pegler & Rayner.

## 7. LENTINUS Fr.

*Stirp. Agri Fems.* 3: 57. 1825, em.

*Type species:* *Lentinus lepideus* Fr. (cf. *Schweiz. Zeitschr. Pilzk.* 29: 211-212. 1951)\*.

*Syn.:* *Lentinula* Earle, *Bull. N. Y. Bot. Gard.* 9: 416. 1909.

*Cryptomphalina* Heim, *Rev. Mycol.* 30: 234. 1966.

*Heliocybe* Redhead, *Trans. Myc. Soc. Japan* 26: 359. 1985.

*Neolentinus* Redhead, l.c. p. 357.

**Characters:** Habit as in the preceding genus; pigment present, but often only in the scales of the pileus, and/or appearing in the carpophores in age on drying (yellow), tan color, cinnamon, fulvous chestnut, ochraceous, etc.; hymenophore usually lamellate, exceptionally irpicoid or with conspicuous anastomoses between the lamellae, adnate or decurrent, edge of the lamellae ± denticulate, lacerate,

\*It is impossible for me to agree with those who wish to typify this genus with *L. crinitus*. The original description by Fries 1821 as well as later descriptions show how poorly he knew and described that species whose type I personally have seen and studied. This whole group does not have conspicuously crenate or dentate lamellae nor has it an odor or is tougher than the European species. It is neither typically purple nor particularly thin-stiped. It is not correct to state that Fries ever considered the tropical species as more typical than the European ones, on the contrary, in the description of the basynonym (*Syst. Mycol.* 1: 174) he indicates "saepe inaequalis et squamosus", lamellae "...margine ...saepe laceratae". "Saepe odorae" which all indicates that he had *L. lepideus* (which is the most squamose, the most lacerate, the most odorous species of the group) in mind, and not the species of the *Crinitus* group which are (1838) actually mainly one (*Panus crinitus*) with synonyms and none of them either squamose or lacerate-gilled, or odorous. In *Epicrisis* where, allegedly, a type selection is made, the character of the dented or lacerate lamellae is even underlined (in italics). In the same paper the genus *Scleroma* is separated, which can only be typified by the one well known species *L. velutinus* which is closely allied to *Panus crinitus*. All this evidence shows that Fries considered *L. lepideus* the central and most characteristic species, not *P. crinitus* and allies. On p. 387 (*ibidem*) he says "lamellis dentatis - genuini *Lentini*" meaning, as is evident, as is evident after what has been pointed out above, that this group also has the dented lamellae (as we have seen not a typical condition) and consequently also belongs to the true Lentini in Fries' sense. Otherwise he would have said "*Lentini Genuini*" as he does in other comparable cases. And finally, in *Hymenomycetes Europaei* where Fries repeats in the diagnosis "lamellae ... acie serrata 1. lacerodentata" and maintains his separation of the *Scleroma*-group because of the entire edge of the lamellae of the latter, he adds (on page 481) that the first and vast section *Criniti* with central stipe is absent in Europe. The word *primaria* in connection with section merely refers to the first place it takes in the previous treatment which includes tropical species (*Epicrisis*) and it cannot be admitted as an argument in typification. It is therefore clear that Fries never designated a type species or even a type section, but on the contrary, gave his basic description in 1821 in such a form as to exclude *Lentinus crinitus* and *L. tigrinus* from the species to be chosen from when it comes to select a type species. This becomes fully clear when we read in *Epicrisis* p. 397: "[*Panus*] a *Lentinis genuinis*, quales omnes Europaei, lamellis ... mox dignoscitur". Since *P. crinitus* is tropical, it is not among the "genuini" Lentini and thus cannot be the type species.

Donk is correctly stating that the type species must be chosen from the basynonym *Agaricus* trib. *Omphalia* subtrib. *Lentiscyphi*. The first selections are those of Earle and Murrill who simply chose the first species (*L. tuber-regium*), a selection which does not have to be followed (Art 8.1) and was superseded by the choice of others (*L. tigrinus*) which is not, as we have seen and was confirmed by Donk (l.c. p. 160 foot note 142), fully representative of the type diagnosis. If Donk considered this argument "not convincing", it derives from his misreading of Fries's words and his insistence on Fries's faulty description of the lamellae of fungi he had never seen fresh or at all. How else could he have described the lamellae of these fungi as equal or subequal? It must be concluded that the only correct choice of a type species is the alternative choice of Konrad & Maublanc (1937, pl. 313), Singer (since 1951), and Singer & Smith 1946: *Lentinus lepideus*.

crenulate, or serrulate, at least in age; hymenophoral trama not completely irregular but regular to subregular in young specimens, its hyphae parallel or somewhat interwoven but always distinctly axillary arranged, later often becoming ± irregular in the mediostratum but with a broad regular lateral stratum (or hymenopodium?), thin-walled at first in many species, but eventually at least many of them becoming thick-walled (wall 0.5-1  $\mu\text{m}$  or more thick); basidia normal in every regard; spore print white to light cream (Ib, Romagnesi); spores hyaline, smooth, inamyloid, ellipsoid-oblong to cylindric, or fusoid, from small to large, with very thin to rather thin simple wall, uni- or binucleate; cystidia absent, or present, with moderately thick walls, with obtuse apices, not always characteristically metuloid, and considerably projecting in most cases; subhymenium either very poorly developed, or more or less strongly differentiated; stipe always present, central to strongly eccentric; veil sometimes present; context fleshy, soon becoming rather tough often reviving when remoistened in situ; hyphae of the trama at least partly thick-walled, inamyloid, with clamp connections\*, the thick walls at times partly gelatinized; hyphal system dimitic or monomitic. On woody substrata, perhaps also on grass roots, often on buried wood, or on charcoal.

*Development of the carpophores:* Secondarily angiocarpous in some species, probably gymnocarpous in others.

*Area:* Almost cosmopolitan (but none of the species as such is cosmopolitan); several species are tropical or subtropical, the rest subtropical and temperate.

*Limits:* It has formerly been thought that *Panus tigrinus* is very closely related to *Lentinus lepideus*. This is not the case. The sterile tissue of the lamellae has a different structure in these species, and the affinities of each of these species are with quite different groups. *P. tigrinus* is so similar to *P. crinitus* that it is often almost impossible to tell the two species apart when they grow together in the American subtropics because *P. crinitus* sometimes becomes glabrous in age under the influence of heavy rains, etc. *L. lepideus*, on the other hand, does not resemble any species of *Panus*. It is closely related to such species as *L. adhaerens*, all species with comparatively thin-walled hyphae in youth, rather thick or rather soft when fresh, and often used for food. All these species have the hymenophoral trama more regular than the species of *Panus*. If all the species with completely irregular hymenophoral trama and developed subhymenium are excluded from *Lentinus*, a group of sections is left that, together, must be admitted as a natural genus, viz. *Lentinus* in the narrow sense. In this sense, the *Lentini* do not include any species with hairy pileus, or with very thin, leathery pileus, or with astipitate carpophores, or with sclerotium, or with ligative hyphae.

Kühner, Lamoure & Fichet (1962) comment that *Lentinus (adhaerens and cyathiformis)* are bipolar and have binucleate spores while *Panus tigrinus* is tetrapolar and has uninucleate spores. According to my own investigations, *Panus crinitus* and *P. tigrinus* have uninucleate and *Geopetalum carbonarium* binucleate spores. It seems that we have here an additional generic difference between the three genera as far as the species are not monomitic.

\*Only in sect. 4 clamp connections (constantly?) rare or absent.

Such aberrant features as originally venose hymenophore, somewhat gelatinized trama, strong characteristic odors, absence of clamp connections, sulcate-pectinate margin of the pileus, or excretion of a resinous mass appear to be restricted to *Lentinus*.

I have restudied the type of the genus *Cryptomphalina*, *C. sulcata* Heim which its author was kind enough to lend me. It has all characters of *Lentinus*, and although it may be a form comparable to the "gasteromycetized" Lentineae, it is also possible that it is only a collection of overaged teratologic forms of a species of *Lentinus*. If inserted in *Lentinus* as an independent species, it must be renamed since a *Lentinus sulcatus* has been published earlier.

*Lentinus* differs from *Pleurotus* as it does from *Panus*, mainly in the structure of the hymenophore. In the cystidiate species, the type of cystidia is rather different. The spore print of *Lentinus* is never livid, but may be white to pale ocher. The number of nuclei in the spores varies in *Lentinus*. The monomitic species are the only ones that have 1-nucleate spores. In *Pleurotus* the monomitic species seem to have 1-nucleate spores and are likewise tetrapolar, but too little is known about the rest of the *Pleurotus* species to compare them in this regard. While the subhymenium in *Pleurotus* is always strongly developed and well differentiated, it is sometimes poorly differentiated in *Lentinus*.

The species of genera of the Tricholomataceae which are more or less pleurotoid differ from *Lentinus* in either shorter, globose to ellipsoid spores and mostly thin-walled hyphae in the regular to subregular hymenophoral trama, evelate stipe and pileus or (for sections 1-4) simply by the monomitic trama. Corner has obscured this difference by including in *Panus* and *Pleurotus* species which do not belong in either of these genera nor to the Tricholomataceae but to the Paxillaceae, and possibly other families (this will be discussed under *Omphalotus* and *Lampteromyces*). He furthermore includes species in *Panus* and *Pleurotus* which are said to have short spores but his spore measurements do not always agree with his drawings (*P. javanicus*) and with the data obtained by other mycologists (*P. giganteus*), or refer to species known only to him and not restudied by others, or are described incorrectly (*P. torulosus*, cf. *Mycologia* 75: 577-8. 1983). In addition, he does not seem to have made up his mind as for the separation of *Panus* from *Pleurotus*, or the position of *Lentinus lepideus* or *Trogia cantharelloides*. Adding to this his preference of *P. crinitus* as type species of *Lentinus* which caused him to introduce a new combination for *Lentinus lepideus*, one is at a loss to understand his argument that a deviation from his choice of type species of *Lentinus* would lead to many new combinations and therefore threatening the stability of nomenclature. Under these circumstances, any changes of the classification or delimitation of the genera here concerned, in the sense of Corner, are not acceptable. They are also not accepted by Pegler (1972, 1983) who combines *Lentinus* with what we call (according to the Code, App. III) *Panus* leaving in *Pleurotus*, as I, some representatives of sect. *Lentodiellum* whereby (1983) it surprises that *P. fockei* (= *P. striatulus*) is characterized by Pegler as monomitic while Corner and I found it to be amphimitic (respectively with "skeleto-binding hyphae"). The same is true for *P. concavus*. There is, furthermore, no doubt but that *Pleurotus dryinus* and at least two species

of the section *Pleurotus* are dimitic so that Pegler's characterization of *Pleurotus* as monomitic and *Lentinus* as di- or amphimitic cannot be maintained.

From all this it must be concluded that the hyphal system as generic character in the Agaricales may lead to results which are not in agreement with the rest of the diagnostically valuable characters, and that hyphal systems, although important on the sectional - sometimes only on the subsectional or specific - level, cannot be used as such for the definition of genera unless they are accompanied by other important characters.

For this reason, the section *Edodes*, differing from other sections in uninucleate spores and monomitic trama, is maintained in *Lentinus* and not transferred (as *Lentinula*) to the Tricholomataceae as proposed by Pegler (1983) who enters it near *Troglia* and *Collybia* (trib. Collybieae) where it has no close relatives.

In *Troglia*, the pileus and hymenophoral trama is monomitic. However, the stipe trama is dimitic according to Corner (1981). This, if true, would show that the "sarcodimitic" tramal structure may pass into truly dimitic trama in some Tricholomataceae, perhaps also in some of the short-spored species described by Corner under *Pleurotus* (e.gr. *P. problematicus* Corner). I do not know any of these species. See also under *Troglia* (p. 307).

*State of knowledge:* The knowledge of the species of *Lentinus* in the present sense is rather complete except for development studies. It would be particularly interesting to extend these studies to all species of *Lentinus*. The author has admitted 14 species. Other species indicated by Saccardo are either synonyms or must be transferred to one of the other genera of the Polyporaceae and Tricholomataceae. Several species are perhaps still undescribed in spite of the large number of names available in the literature.

*Practical importance:* Several species of *Lentinus* have a considerable economic value, e.gr. *L. edodes*, a species widely used in oriental cooking, and sold in fresh, dried, and canned condition in China, Japan, and everywhere where Chinese and Japanese live, even all through the Malays and the Philippines. This species is grown commercially in China and Japan; in Japan, the methods\* are now based on scientific results, and the yield has subsequently increased; in China, the growing is still primitive. It is done by watering old trunks of *Pasania* and oak in a neighborhood where *L. edodes* grows wild. The Japanese growers now rely on pure cultures. The fungus is known as *shiitake* (Japanese). Another edible fungus of this genus is *L. glabratus*.

*L. kauffmanii* appears to be one of the two most dangerous parasites on living conifers in British Columbia, especially on *Picea sitchensis* and other commercially important lumber trees. It causes brown pocket rot.

Several species of *Lentinus* inflict considerable damage to wooden structures and building material. The most important wood-destroyer (though practically limited

\*See Singer, R. *Mushrooms and Truffles*. Leonard Hill, London NW 1. 1961 (World Crops Books) and Tatsuzino Ito in Chang & Hayes, *Biology and Cultivation of edible mushrooms*, Academic Press, 1978.

to coniferous wood) is *L. lepideus*. It is often very common on railway ties, on bridges, even on wooden houses on wood used in mines.

*L. edodes* contains an antibiotic, cortinellin (Hermann, *Naturwiss.* 49: 52. 1962). This and *L. lepideus* contain anti-tumor substances e.gr. a polysaccharide (lentinan) according to Ikekawa et al. (*Cancer Res.* 29: 734-5. 1969). Lentinan has been reported as acting immunologically as a T-cell adjuvant (Dennert & Tucker, *Journ. Nat. Cancer Inst.* 51: 1727-9. 1973 and Maeda & Chihara, *Nature* (London) 229: 634. 1971). *L. edodes* has also been reported to have an anti-viral effect against para-myxo- and other viruses (Yamamura & Cochran, *Mushroom Science* 9: 495-507. 1976). The same species is believed to lower plasma cholesterol in animal experiments due to eritodenine, a substance discovered by some Japanese authors (cf. Cochran in Chang & Hayes, *The Biology and Cultivation of edible mushrooms* 1978)

## SPECIES

Subgenus I. **Lentinus.** Hyphal system mostly dimitic. Spores binuclear. Usually bipolar. Brown rot.

*Type species:* As in genus.

Sect. 1. **VARIABILES** Sing. (1948). Lamellae at first obtuse and venose, gradually broadening and reaching full size only at or after full maturity, the broadening taking place by the way of a growth line along the edge of the lamellae which consists of actively dividing hyphal elements which are often similar to cheilocystidia; hymenophoral trama subirregular in the upper part, at least in the mature specimens, subregular in the portion near the edge, rather loosely arranged, consisting of filamentous, often rather thick-walled hyphae; the subhymenium moderately well developed, comparatively loose, not thick; metuloids and lamprocystidia none; clamp connections present; veil none; margin not sulcate; hyphal structure dimitic.

*L. cyathiformis* (Schaeff. ex Fr.) Bres. (*L. variabilis* Schulzer apud Quél.; *L. degener* Kalchbr. apud Fr.).

Sect. 2. **LENTINUS** [Squamosi Fr. (1863); Mesopodes subsect. Lepidei Fr. 1874]. Lamellae not venose for a long time; hymenophoral trama regular, consisting of moderately thick-walled hyphae which are subinterwoven in the central portion of the trama (mediostratum) and more strictly parallel near the subhymenium or the hymenium; subhymenium either negligible or well developed, consisting of thin, small hyphae, rameous, with crowded septa; metuloids or lamprocystidia present or absent; veil present or absent; hyphal structure dimitic; clamp connections present; margin not sulcate; often odoriferous\*.

*Type species:* *L. lepideus* Fr.

\*The strong odor of *L. lepideus* is due to the formation of methyl-cinnamate.

*L. lepideus* (Fr. ex Fr.) Fr.; *L. spretus* Peck; *L. ponderosus* O. Miller. - *L. adhaerens* (A. & S. ex Fr.) Fr.; *L. kauffmanii* A.H. Smith.

Sect. 4. *FULVIDI* Sing. (1943). Hymenophore not venose in youth; hymenophoral trama regular or subregular in young specimens, at least near the edge, consisting of thick-walled and some thin-walled filamentous hyphae and some connective hyphae; subhymenium little developed; metuloids (lamprocystidia) present or absent; clamp connections absent or few; veil present, but little developed; margin of the pileus deeply sulcate; pigment of the cuticle of the pileus abundant, yellow (fulvous macroscopically). Hyphal system mono- or dimitic.

Type species: *L. fulvidus* (Bres.) Pilát.

*L. fulvidus* (Bres.) Pilát (Panus, Bres.); *L. sulcatus* Berk. (*Russula pringlei* Robinson; *Lentinus misericulus* Kalchbr.)

Subgenus II. *Edodes* st.n. (*Edodes* as section, Sing. *Sydotia Beih.* 7: 1. 1973). Hyphal system monomicic. Spores uninuclear. Usually tetrapolar.

Type species: *L. edodes* (Berk.) Sing.

Sect. 5. *EDODES* Sing. (1973). Characters as in subgenus.

Type species: As in subgenus.

*L. boryanus* (Berk. & Mont.) Sing. (*Collybia*, Sacc.; *Lentinula*, Pegler; *Lentinus detonsus* Fr.; *Lentinula*, Murr.; *Panus leprieurii* Mont.; *Agaricus ixodes* Mont.; *Lentinus cubensis* Berk. & Curt.; *Lentinula*, Earle; *Lentinus proximus* Berk. & Curt.; *Armillariella umbilicata* Pat.; *Armillaria*, Sacc.); *L. sayanus* Sing.; *L. puiggarii* Speg.; *L. panziensis* Sing.; *L. guarapiensis* Speg.; *L. edodes* (Berk.) Sing. (*Agaricus*, Berk.; *Armillaria*, Sacc.; *Cortinellus*, S. Ito & Imai; *Collybia shiitake* Schröter; *Tricholoma*, Ramsbottom).

## 8. GEOPETALUM Pat.,

*Hymen. Europe* p. 127. 1887.

Type species: *Cantharellus carbonarius* A. & S. ex Fr.

Syn.: *Faerberia* Pouzar, Česká Mykologie 35: 187. 1981\*

\*Pouzar proposed *Faerberia* because he considered *Geopetalum* a superfluous name (Art. 63). Art. 63.2 modifies "... unless the type (of a name or epithet that should have been adopted under the rules, i.e. *P. petalooides* and *implicite* the generic name *Hohenbuehelia*) is at the same time excluded either explicitly or by implication". Patouillard, in his original description excludes *H. petalooides* by indicating the spores as ovoid-allongées while they are not elongated ("remarkably short" Kühner) in *H. petalooides*. Furthermore, if the genus *Geopetalum* were superfluous another sentence of the same article excepts this case by saying "... unless the author of the superfluous name or epithet has indicated a definite type". This, Patouillard did by excluding in a later publication the *Hohenbuehelia*s thus indirectly narrowing the choice of type to *G. carbonarium*. Earle's so-called first lectotypification is not only nine years later than Patouillard's own but it was made by misinterpreting the protologue and does not have to be followed because it was not binding according to Art. 8.1. We adhere therefore to the lectotypification by Donk, Singer & Smith and others which is also that of Patouillard. If the type of a genus is a specimen or an illustration, the type of *Geopetalum* may well be Patouillard, *Hymen. Pl. III*, fig. 9. 1887.

**Characters:** Habit clitocyboid, but at times somewhat eccentrically stipitate and pileus strongly depressed; cuticle consisting of hyphae which form indistinct floccos consisting of a trichodermium but becoming very strongly applanate at least in their outermost layer and consequently appearing dense, pigmented with a stramineous to brown intracellular pigment but the hyphal walls also pigmented (same color), smooth, terminal cells often in form of versiform, thick- or thin-walled dermatocystidia; hymenophore lamellate-venose; lamellae very narrow and obtuse and usually strongly forked, decurrent, arcuate or straight descendant, dull cremeous to dull cinerous in age; spore print color not known, supposedly white; spores hyaline, smooth, cylindric, cylindric-ellipsoid-oblong to recurved (i.e. sausage-shaped with the inner side convex and the outer side concave), asymmetric, inamyloid, with rather thin, simple acyanophilous wall, binucleate; basidia usually 4-spored, some 1-, 2-, or 3-spored, narrower than the length of the spores and 4-4.5 times as long as the length of the spores; metuloids shaped like those of *Pleurotus* and *Hohenbuehelia*, pseudoamyloid, with crystalline incrustation in the free portion, acute or subacute at the apex, strongly metachromatic (pinkish lilaceous on blue to violet background provided by the basidia in cresyl blue, lilac-pink in toluidin blue) and slightly cyanophilous; subhymenium present, slightly colored (the trama being hyaline), consisting of very small and short elements; hymenophoral trama subirregular, many of the hyphae thick-walled, denser in the mediostratum; pileus and hymenophoral trama inamyloid, dimitic; stipe often subradicant, without veil, central or eccentric, more or less vertical, solid; context fleshy-tough, not soft nor watery, consisting of thin- to thick-walled nonamyloid hyphae with clamp connections, without gelatinous layer. On charcoal.

**Development of the carpophores:** Gymnocalypous according to Reijnders.

**Area:** Europe.

**Limits:** The somewhat tough, dry consistency, the presence of typical pseudo-amyloid metuloids, the vein-like character of the hymenophore, and the absence of a gelatinous layer in the context are sufficiently important characters to separate *Geopetalum* generically from the genera of the *Resupinateae* as well as from those of the *Lentineae*. The author has transferred this genus to the latter tribus because of the absence of a gelatinous layer, and the elongate spores tending to be recurved. The presence of metuloids alone would not be sufficient reason to consider this genus as related with or identical with *Hohenbuehelia*, inasmuch as some species of *Pleurotus* have very similar metuloids. The venose character of the hymenophore can be compared with that of *Lentinus cyathiformis* in immature specimens.

Singer and Cléménçon have shown (1973) that *Geopetalum* is indeed, as stated by Corner (1966), dimitic (with skeletals) and has endocystidia. In spite of the monomitic hyphal structure in the Hohenbuehelias and their frequently short, broad spores, there is some similarity between *Hohenbuehelia*, especially *H. longipes*, and *Geopetalum*, but the latter is not gelatinized in the pileus and stipe, and has pseudo-amyloid cystidia whereas *Hohenbuehelia* has characteristic cheilocystidia and a more distinctly lamellate hymenophore. While some Hohenbuehelias have rather elongated spores, more species have ellipsoid or short ovoid spores. While it is

certain that these differences confirm that these genera belong in different families, the similarity between *Geopetalum* and *Hohenbuehelia*, like that between *Pleurotus* and *Clitocybe* suggests that putting them in different orders would be going too far.

Kühner who combines our genus *Pleurotus* and *Panus* including the *Lentinus* in the sense of Corner into a single genus which he calls “*Pleurotus* (Fr.) Quél. sensu Kühner (1926) emend.” (and which, if accepted with this circumscription should be called *Panus*!) also combines *Lentinus* and *Geopetalum*. Here as in many other cases the size of the genera in Kühner’s classification (1979) is a very wide one, adapted to his personal concept of the genus in Agaricales, but he expressed the affinities very well since clearly the nearest relative of *Geopetalum* is indeed *Lentinus*, not *Pleurotus* as Corner seems to think (1966) but later corrected (“its place in the Agaricales is anomalous”) in 1981.

*State of knowledge:* Only one species is referable to this genus.

*Practical importance:* Unknown.

## SPECIES

*G. carbonarium* (A. & S. ex Fr.) Pat. (*Merulius* (A. & S. ex Fr.) Pers.; *Cantharellus umbonatus* var. *carbonarius* (A. & S. ex) Fr.; *C. anthracophilus* Lév.; *C. radicosus* Berk. & Br.; *Merulius leucophaeus* Pers.).

## HYGROPHORACEAE Roze

(ut Hygrophorées) *Bull. Soc. Bot. Fr.* 23: 51. 1876, nom. nud.; *ibid.*, p. 110. 1876; R. Maire, (ut Hygrophoracées) *Bull. Soc. Myc. Fr.*, Tabl. 1901, nom. nud.; *Rech. cyt. et tax. sur les Basidiomycètes*, Paris p. 114. 1902; Lotsy, *Vortr. Bot. Stammesgesch.*, p. 706. 1907.

*Type genus:* *Hygrophorus* Fr., *Gen. Hym.*, p. 8, 1836.

*Characters:* Pileus often viscid to glutinous, the cuticle consisting of radiately arranged, filamentous hyphae, often dense, more rarely consisting of repent or erect hyphae which are imbedded in a gelatinous mass or of swollen elements forming a hymeniform layer; hymenophore lamellate; lamellae waxy and thick (not obtuse unless they are so because of a glutinous layer at the edge) mainly because of the unusual length of the basidia (5.2-7 times as long as the spores); basidioles filamentous; sterigmata four, or two; spores thin-walled, small and globose to voluminous and cylindric, most frequently rather inconstant in size (or even di- or trimorphic) and shape and approximately ovoid-ellipsoid (cylindric), always smooth, rarely stellate-echinate, inamyloid, rarely amyloid (and then lamellae distant, purplish drab, and decurrent; veil none; hymenophoral trama intermixed irregular, red in KOH), acyanophilous when young; cystidia none, or rather inconspicuous; basidia without siderophilous granulation; hymenophoral trama irregular to intermixed, or regular, or bilateral; stipe subcartilaginous to fleshy, sometimes viscid or glutinous, sometimes veiled, smooth or furfuraceous-fibrillose

at the apex or longitudinally-striate-fibrillose all over (the veiled forms always with bilateral hymenophoral trama); context mild or sometimes bitter, not acrid, usually fleshy in consistency at least in the pileus; hyphae always inamyloid, with numerous clamp connections, more rarely (constantly in *Hygroaster* and *Humidicutis*) without clamp connections; trama homoiomericous without separation-zones and never horny or chordaceous. Always monomitic. On the ground in woods (mycorrhizal only in *Hygrophorus*), among mosses (frequently among *Sphagnum*), more rarely on decayed wood, charcoal, frequently also outside the forest from sea level to the alpine zone, almost cosmopolitan.

**Limits:** There are other groups with thick lamellae (e.gr. *Laccaria*), not directly related to the Hygrophoraceae. In *Laccaria* the basidia are less than 5.5 times longer than the spores. There are also species with rather thick lamellae described in *Dermoloma*; they have, however, basidia less than five times as large as the length of the spores - which are amyloid - and do not seem to be more closely related to *Neohygrophorus* than to *Dermoloma*.

The genus *Hygrophorus* may come close to *Clitocybe*. In some species of *Clitocybe* a rather distinct divergence of the almost regular hymenophoral trama in its outer regions can be observed, and then the tramal structure may be considered as somewhat transitory. In this case, the viscosity of the pileus, a character rare in *Clitocybe*, the relative size of the basidia, the presence or absence of a veil (no veil in *Clitocybe*) will decide. In general, the distinction is very easy, even to the beginner, or at least becomes evident after some experience. The delimitation of *Clitocybe* and *Hygrophorus* does not represent a taxonomic problem. *Hygrophorus russula* has often been considered as a *Tricholoma* but without the slightest justification.

In the tribus *Hygroastreae* the basidia may not always reach the length required in the Hygrophoraceae, but this is also the case in some exceptional species of *Hygrocybe* which, having all the other characters of that genus, cannot be separated from it. Kühner thinks that the genus *Omphaliaster* should be transferred to the Tricholomataceae. He states however that "Singer without doubt is right synonymising *Omphaliaster* and *Hygroaster*." This confirms the opinion that both genera must remain in the same family - and my own measurements of the basidia and spores of the type species of both genera tend to indicate that this should be the Hygrophoraceae.

The genus *Gomphidius* has been considered as belonging in this family by some mycologists, or has at least been considered as closely related because of the thick waxy lamellae and the long basidia. However, the absence of clamp connections, the deep colored spores, the cystidia of the bolete type, the chemical reactions, and many other characters show that the Gomphidiaceae are closer to the Boletaceae than to the Hygrophoraceae.

The tribus *Biannularieae* of the Tricholomataceae also has bilateral trama. However, it also has a double veil, amyloid spores, and close to crowded lamellae, a combination of characters that is foreign to the Hygrophoraceae proper.

The genus *Asterophora* which was considered by some as belonging to the Hygro-

phoraceae is distinguished by the siderophilous granulosity of its basidia. The same character can serve as a safe means of distinguishing between all *Lyophylleae* (Tricholomataceae) which tend to have rather long basidia at times, and the Hygrophoraceae.

#### KEY TO THE TRIBUS

- A. Spores smooth, exceptionally with an ornamentation of type XI (light microscope), not nodose or stellate; clamp connections present or absent
  - B. Hymenophoral trama bilateral; veil often present; lamellae  $\pm$  decurrent; always ectomycorrhizal; clamp connections present.  
*Hygrophoreae* (p. 192)
  - B. Hymenophoral trama irregular to regular, not bilateral; lamellae decurrent or not; not ecto-mycorrhizal.  
*Hygrocybeae* (p. 195)
- A. Spores nodose or stellate but with homogeneous wall; clamp connections a  
*Hygroastreæ* (p. 207)

#### Tribus *Hygrophoreae* (autonym)

Type and only genus: *Hygrophorus* Fr.

Characters: as indicated in the key above.

#### 9. HYGROPHORUS Fr.

Genera Hymenomyc., p. 8. 1836, em. Karst.

Type species: *Hygrophorus eburneus* (Bull. ex Fr.) Fr.

Syn.: *Limacium* (Fr. ut tribus) Schroeter in Cohn, Krypt.-Fl. Schles., Pilze, p. 530. 1889.  
*Limacium* Kummer, Führ. Pilz., p. 25. 1871.

Characters: Those of the family. Lamellae, adnate-subdecurrent to deeply decurrent; hymenophoral trama bilateral; veil often present; cystidia very rare, and then inconspicuous; pseudocystidia none; spores inamyloid. Usually growing in the neighborhood of trees and forming mycorrhiza with various genera of Cormophyta.

Development of the carpophores: Gymnocalyx in some species, but secondarily-angiocarpous (mixangiocarpous in others).

Area: Northern hemisphere, not passing beyond the *Quercus*-area in Central and South America, also Southern Hemisphere temperate zone, but absent in temperate South America.

Limits: The key characters provide a satisfactory delimitation.

State of knowledge: Thanks to the efforts of many mycologists in Europe (recently by Bresinsky & Huber 1967 who provided a key to the dried specimens, Orton, Kühner, Moser, Kühner & Romagnesi, and others) and in North America (A.H.

Smith, Smith & Hesler and Hesler & Smith), the species of *Hygrophorus* can be considered as rather well known. Below 53 species are listed.

**Practical importance:** As obligatory ectomycorrhizas, which are rather selective in most cases, the genus may become important in forestry. All species known (excepting probably *H. pusillus* which is said to contain an alkaloid) are edible (as far as tested), and *H. marzuolus* a spring species occurring in the mountain forests of *Abies* and perhaps other conifers, is often seen in the markets in Switzerland.

## SPECIES

Sect. 1. **HYGROPHORUS** (*Candidi* Bat. 1910). Pileus without pigment, or slightly pigmented (colored pale ochraceous or pale tan on the disc only, rarely becoming deeper colored when dried properly).

*Type species:* *H. eburneus* (Bull. ex Fr.) Fr.

Subsect. **Chrysodontini** Sing. (1943). Veil not gelatinous-glutinous (i.e. not consisting exclusively of a colorless glutinous mass) but floccose or almost cortinoid and dry.

*Type species:* *H. chrysodon* (Batsch ex Fr.) Fr.

*H. chrysodon* (Batsch. ex Fr.) Fr.; *H. quercuum* Sing. and several other, somewhat imperfectly known species.

Subsect. **Pallidini** Smith & Hesler (1939). Veil absent and stipe dry to somewhat moist, and at times subviscid-slippery to the touch.

*Type species:* *H. sordidus* Peck.

*H. subalpinus* A.H. Smith; *H. sordidus* Peck; *H. subsordidus* Murr.; *H. karstenii* Sacc. & Cub.; *H. albidus* Karst.; *H. pusillus* Peck, and probably also *H. penarius* Fr.

Subsect. **Hygrophorus** (*Albidi* Sm. & Hesl.). Stipe with a viscid veil, without a dry cortinoid veil, and without a zone of floccos at the apex forming a velar zone.

*Type species:* *H. eburneus* (Bull. ex Fr.) Fr.

*H. ponderatus* Britz. sensu Sm. & Hesl.; *H. gliocyclus* Fr., *H. flavodiscus* Frost apud Peck, *H. rubropunctus* Peck; *H. eburneus* (Bull. ex Fr.) Fr.; *H. cossus* (Sow. ex Fr.) Fr. (*H. subpurpurascens* All.; *H. eburneolus* Britz.; *H. chrysaspis* Métrod).

Sect. 2 **PUDORINI** (Bat. ut subsectio) Konr. & Maubl. (1924- 1937). Pileus pink, pale pinkish tan, brownish rose, salmon color, pinkish buff, sometimes tending towards tawny, russet or cinnamon, or even as dark as clay color or tawny olive (both in the sense of Ridgway), Kaiser brown, cameo brown, etc. Stipe without a glutinous veil or coating.

*Type species:* *H. pudorinus* (Fr.) Fr.

Subsect. *Erubescentes* Sm. & Hesl. (1939). Lamellae with vinaceous purple or pink or testaceous tinge in age, or becoming maculate in these colors.

Type species: *H. erubescens* (Fr.) Fr.

*H. purpurascens* (A. & S. ex Fr.) Fr.; *H. russula* (Schaeff. ex Fr.) Quél.; *H. russuliformis* Murr.; *H. proximus* Krieger; *H. amarus* Sm. & Hesl.; *H. erubescens* (Fr.) Fr.; *H. kauffmanii* Sm. & Hesl.; *H. nemoreus* (Lasch) Fr.

Subsect. *Fulvoincarnati* Sm. & Hesl. (1939). Lamellae white to cream color, occasionally flushed pale pink but usually not in the colors indicated for subsection *Erubescentes*, most frequently white or whitish and not spotted.

Type species: *H. pudorinus* (Fr.) Fr.

*H. pudorinus* (Fr.) Fr.; *H. fragrans* Murr. (if really different from *H. pudorinus*); *H. queletii* Bres.; *H. pacificus* Sm. & Hesl.; *H. bakerensis* Sm. & Hesl.; *H. tennesseensis* Sm. & Hesl.; *H. laricinus* Peck; *H. subisabellinus* Sm. & Hesl.; *H. subrufescens* Peck; *H. roseibrunneus* Murr.; *H. arbustivus* Fr.

Sect. 3. *DISCOIDEI* (Bat. ut subsectio) Konr. & Maubl. (1924-1937). (Subsect. *Lutei* Sm. & Hesl.; *Brunnei* Sm. & Hesl. 1939). Pileus yellow to red, orange, tawny, russet, or dark pinkish tan, sometimes with a flush of olive mixed with the above colors, and sometimes fuscous but then the lamellae yellow; stipe more or less viscid, often with a purely glutinous veil.

Type species: *H. discoideus* (Pers. ex Fr.) Fr.

*H. lucorum* Kalchbr.; *H. speciosus* Peck; *H. hypothejus* (Fr.) Fr. [with var. *aureus* (Arrh. apud Fr.) Imler]; *H. subsalmonius* Sm. & Hesl.; *H. discoideus* (Pers. ex Fr.) Fr.; *H. vernalis* A.H. Smith; *H. leucophaeus* (Scop. ex Fr.) Fr.; *H. laurae* Morgan; *H. variicolor* Murr.; apparently also *H. spodoleucus* Moser and *H. lindtneri* Moser.

Sect. 4. *COLORATI* Bat. (1910), em. [*Olivaceoumbrini* (Bat. ut subsectio) Kor. & Maubl. (1924-1937). *Limacium* sect. *Communia* Sing. 1943]. Pileus olivaceous to fuligineous gray, grayish fuscous.

Type species: *H. olivaceoalbus* (Fr.) Fr.

Subsect. *Olivaceoumbrini* Bat. (1910). (*Euhygrophorus* subsect. *Fuliginei* Sm. & Hesl. 1939.) Stipe with a viscid coating of velar origin that is more or less colorless and thoroughly glutinous.

Type species: *H. olivaceoalbus* (Fr.) Fr.

*H. olivaceoalbus* (Fr.) Fr. (also allied species; their relationship is not fully understood at present, at least, the authors do not fully agree as to their synonymy); *H. fuligineus* Frost in Peck; *H. paludosus* Peck; *H. olivaceonitens* (Sing.) Sing. (*Limacium*, Sing. 1943); *H. megasporus* Sm. & Hesl.; *H. occidentalis* Sm. & Hesl.; *H. limacinus* (Scop. ex Fr.) Fr.; *H. fuscoalbus* (Lasch) Fr.

Subsect. *Tephroleuci* Bat. (1910). (Sect. *Clitocyboides*, subsect. *Atrocinerei* Sm. & Hesl. 1939; subsect. *Camarophyllini* Hesl. & Sm.; *Limacium*, sect. *Communia*

subsect. *Tephroleucini* Sing. 1943; *Camarophyllus*, sect. *Caprini* Bat. 1910; *Hygrophorus* sect. *Tephroleuci* and *Caprini* Konr. & Maubl. 1924-1937). Veil if present, not completely glutinous, mostly absent and then the stipe dry, rarely subviscid and somewhat slippery to the touch.

Type species: *H. agathosmus* (Fr.) Fr.

*H. agathosmus* (Fr.) Fr.; *H. pustulatus* (Pers. ex Fr.) Fr.; *H. marzuolus* (Fr.) Bres.; *H. camarophyllus* (A. & S. ex Fr.) Dumée, Grandjean & R. Maire [Agaricus, Fr. 1821; *Hygrophorus caprinus* (Scop. ex Fr.) Fr.; *Camarophyllus*, Kummer; *Limacium*, Kühner; *H. calophyllus* Karst. [*H. camarophyllus* var. *calophyllus* (Karst.) Konr. & Maubl.; *H. caprinus* var. *calophyllus* (Karst.) Quél.; *Limacium calophyllum* (Karst.) Sing.] - apparently also *H. hyacinthinus* Quél.].

Note: *H. tephroleucus* (Fr.) Fr. in the sense of some authors is very close to *H. pustulatus*, hence of this subsection (and the subsectional name has therefore been used for it). Others think of it as coinciding with a form belonging in subsection *Olivaceoumbrini*. If this were correct, the subsectional name of the present group would have to be changed.

### Tribus *Hygrocysteae* Kühn.,

Bull. Soc. Linn. Lyon 48: 621. 1979.

Type genus: *Hygrocyste* Kummer

Characters: As indicated in key (p. 192)

### KEY TO THE GENERA

- A. Spores amyloid; hymenophoral trama reddening in KOH
- A. Spores inamyloid
  - B. Clamp connections in the hyphae of the carpophore present (though at times rather scattered)
    - C. Epicutis - a trichodermial palisade to hymeniform, at least over part of the pileus surface
      - 11. *Hygrotrama* p. 198
      - C. Epicutis - a cutis, ixocutis or ixotrichodermium, often poorly differentiated; if there is a trichodermium it consists of non-inflated filamentous hyphae
      - D. Hymenophoral trama at least in part (near trama of pileus) strictly irregular (subparallel hyphae may be present in the mediostratum and/or in the hymenopodium), interwoven, consisting of narrow (mostly 3-5, rarely up to 8  $\mu\text{m}$  broad) hyphae; lamellae adnate to decurrent; bright colored, dissolved intracellular pigment (yellow, red, pink, parrot green, blue) absent (but occasionally lilac-livid, cream-salmon or dusky olive pigmentation present in the surface of the pileus or yellow pigments in the base of the stipe).
        - 10. *Camarophyllus*, p. 196
        - D. Hymenophoral trama entirely consisting of very broad hyphae or hyphae at least mainly broader than indicated above, and these arranged either regularly and parallel with each other or slightly interwoven but axially arranged; lamellae varying from adnexed to decurrent, often irregularly attached; bright colors observed in the majority of the species either on both pileus and stipe or on lamellae (or both).
          - 13. *Hygrocyste*, p. 202
  - B. Clamp connections absent even in 4-spored forms and in the subhymenium

- E. Bright colored pigments absent, rarely colors with salmon pink or greenish tones; hymenophoral trama regular to irregular
- F. Epicutis hymeniform or at least trichodermial over a large part of the pileus, consisting of rather broad elements, or at least with recurved hyphal elements in the marginal zone, with numerous multiseptate elements present (and then a slight veil visible in young carpophores); hymenophoral trama regular or subregular (see *Hygrotrama*, p. 198)
- F. Epicutis - an ixotrichodermium or an ixocutis, or, if not gelatinized, neither hymeniform nor a trichodermial palisade, nor with the hyphae recurved in the upper marginal zone and without any trace of a veil (gymnocarpous), or if there is a slight veil, it is glutinous; hymenophoral trama regular to irregular (see "D" above)
- E. Bright colored: orange, red, salmon, yellow pigment present on the pileus and/or stipe and lamellae (or both), on pileus often only in radial streaks; hymenophoral trama not irregular
- G. Cortical layer of pileus and/or stipe gelatinized or else pileus neither conical nor squamulose but glabrous (not innately fibrillose or streaked); bright pigments easily washed out and surface bleaching in 5% KOH (see "D" above)
- G. Cortical layer of pileus and stipe not gelatinized and pileus at least in certain stages tending to be conical or pulvinate, often fibrillose or tending to become squamulose. Lamellae never decurrent, always white to golden yellow or orange.

14. *Humidicutis* p. 206

## 10. CAMAROPHYLLUS Kummer

*Führ. Pilz.*, p. 26, 1871.

Type species: *C. pratensis* (Pers. ex Fr.) Kummer\*.

Syn.: *Agaricus* trib. *Clitocybe* subtrib. *Camarophyllus* Fr., *Syst. Myc.* 1: 98. 1821.

*Hygrophorus* tribus *Camarophyllus* Fr., *Epicr.* p. 325. 1838.

*Camarophyllus* (Fr.) Karst., *Bidr. Finl. Nat. Folk* 32: xvii. 1879.

*Hygrocybe* subg. *Cupophyllus* Donk, *Beih. Nov. Hedw.* 5: 45. 1962.

*Hygrophorus* sect. *Camarophyllopsis* Hesl. & Sm., *Hygr.*, p. 48. 1963, non genus

*Camarophyllopsis* Herink 1959, nec *Hygrotrama* subgenus *Camarophyllopsis* (Herink) Sing. (1972).

*Aeruginospora* Höhnel, *Sitz.-ber. K. Akad. Wiss. Wien, Math.-Naturw. Kl.* 117: 1012. 1908.

Characters: Those of the family; pileus not very brightly colored in the red and yellow colors of *Hygrocybe*, rarely with salmon cream or greenish colors (but then without clamp connections), or with violet colors (but then combining clitocyboid habit and non-viscid pileus), occasionally with an olivaceous hue, but basically dull colored all over (the base of the stipe might be yellow at times) or lacking pigments entirely. Habit mostly clitocyboid. Hymenophoral trama distinctly irregular or, if axially arranged hyphae predominate, these are narrow 3-5-(8)  $\mu\text{m}$  broad or occur only in one part of the hymenophore which is however more often homogenous than distinctly differentiated into a mediostratum and a lateral stratum. Veil absent. Basidia normal and always relatively long. Cystidia usually absent in all forms and shapes. Pigments, if present, most frequently intracellular and dissolved, less

\*There is no indication in the Code of nomenclature which would force us to choose the type species according to tautonomy of the genus and a specific epithet once used in the genus. Since selection of a type species is not achieved by designating a first species (Earle, Murrill), the first selections which must be followed are Konrad's (1934) and Singer's (1951), the latter for *Camarophyllus* Kummer. Hesler & Smith (1963) base their section *Camarophyllopsis* on *Camarophyllus* "(Fr.)" Kummer, again with the type species: *C. pratensis*. If *A. camarophyllus* A. & S. were acceptable as type species, the name of the genus now based on *C. pratensis* would be *Aeruginospora* Höhnel.

frequently intraparietal and incrusting (in addition). Hyphae with or, more rarely, without clamp connections (but then basidioles binucleate and/or basidia 4-spored; bisporous forms frequently clamp-less). Epicutis formed by a cutis, ixocutis, ixotrichodermium or a trichodermium of narrow hyphae. Spores smooth, with homogenous and thin wall, often short, inamyloid, acyanophilous, hyaline, typically uninucleate, at least in their majority, in the species cytologically studied. - On the ground in and outside the woods.

*Development:* Gymnocalypous.

*Area:* Almost cosmopolitan.

*Limits:* The hymenophoral trama, combined with the characters of the cuticular layer of the pileus, the habit and pigments, make this a homogenous genus, rather easily distinguished in the field and laboratory. The clamp-less species are few and should not be confused with the *Omphalinae* where the parthenogenetic forms are often those with clampless hyphae and, of course, the basidia are relatively shorter. The spores were always found to be hyaline. The greenish spore print of *Aeruginospora* has not been confirmed by Dutch collectors who annotated topotypical material (L) of *A. singularis* as having *absolutely white* spore print (even though light sea green (K & V) lamellae). Höhnél's indication to the contrary must be considered an error. The type has hyaline spores. Since I have collected and described one clamp-less species in the typical *Camarophyllus* group, and all other characters of *A. singularis* are those of *Camarophyllus*, I consider *Aeruginospora* to be a synonym of *Camarophyllus*.

*State of knowledge:* 28 species are well known.

*Practical importance:* Only *C. pratensis* is widely known as edible.

## SPECIES

Sect. 1. *VISCIDI* (Hesl. & Sm.) Sing. (1972). Dull colored (gray, umber, sometimes more cinnamon or with vague violet shades and then with an ixocutis). Clamps present. Base of stipe not yellow.

*Type species:* *H. subviolaceus* Peck.

*C. subviolaceus* (Peck) Sing.; *C. colemanianus* (Blox. ex Fr.) Ricken; *C. recurvatus* (Peck) Murr. (*Clitocybe praticola* Murr.; *Omphalina australis* Murr.); *C. cinereus* (Fr.) Karst. (at least a subalpine European form studied by me); *C. subradiatus* (Schum. ex Fr.) Wünsche; *C. hieronymi* Sing.; *C. rainieriensis* (Hesl. & Sm.) Sing.; *C. canescens* (Sm. & Hesl.) Sing.; *C. tehuelches* (Speg.) Sing.; *C. umbrinus* (Dennis) Sing. (see note).

*Note:* Some of these species are non-viscid and have no appreciable ixocutis. The non-viscid species may be separated in a special subsection or series (e.g. *C. canescens* and following species including *Hygrophorus umbrinus* Dennis, *Kew. Bull.* 2: 257. 1953 in spite of well differentiated mediostratum of subparallel

hyphae, and some other species (see *Sydowia* 30: 272. 1977).

Sect. 2. *VIRGINEI* (Bat.) Sing. (1972). Pileus white or, if buffy cream, with an ixocutis.

Type species: *H. virgineus* (Fr.) Fr.

*C. niveus* (Scop. ex Fr.) Karst.; *C. borealis* (Peck) Murr. (if different from *C. niveus*); *C. virgineus* (Wulf. in Jacq. ex Fr.) Kummer; *C. niveicolor* (Murr.) Sing.; *C. buccinulus* Sing.; *C. angustifolius* Murr.; *C. russocoriaceus* (Berk. & Miller) Lange; apparently also *H. berkeleyi* Orton.

Sect. 3. *CAMAROPHYLLUS*. Pileus cinnamon to orange-buff, rusty buff. Epicutis if developed, not an ixocutis; pileus not or scarcely viscid.

Type species: *C. pratensis* (Pers. ex Fr.) Kummer

*C. cremeus* (Murr.) Sing.; *C. cremicolor* Murr.; *C. pratensis* (Pers. ex Fr.) Kummer; *C. fulvosiformis* Murr.; *C. ferrugineoalbus* (Sing.) Sing. (Clitocybe, Sing.; *Omphalia bicolor* Baker & Dale; Clitocybe, Dennis).

Sect. 4. *ADONIDI* Sing. (1972). Pigments different from the preceding section: bright lilac-violet pigments present, otherwise like sect. 3. Base of stipe mostly yellow, or lamellae amethyst color.

Type species: *C. adonis* Sing.

*C. adonis* Sing.; *C. grinnlingii* Sing.; *C. lacmus* (Fr.) Lange; *C. laccaroides* Sing.

Sect. 5. *AERUGINOSPORA* (Höhn) Sing. (1972). Differs from the preceding sections in the absence of clamp connections.

Type species: *A. singularis* Höhn

*C. patagonicus* Sing.; *C. singularis* (Höhn.) Sing.; *C. paraiboensis* Sing.

## 11. **HYGROTRAMA** Sing.

*Sydowia* 12: 221. 1959 (March).

Type species: *H. dennisianum* Sing.

Syn.: *Hodophilus* Heim ex Herink, *Acta Mus. Boh. sept. Liberac.* 1: 61. 1959 (July).

*Camarophyllopsis* Herink, l.c., distributed July 1959, Art. 29.1.

*Hygrocybe* sect. *Hygromyces* (Sing.) Orton & Watling, *Not. R. Bot. Gard. Edinburgh* 29: 134. 1969.

*Hygrophorus* sect. *Hygromyces* (Sing.) Hesler & Smith, *Hygroph.* p. 96. 1963.

Characters: Those of the family. Lamellae adnate to decurrent; habit more or less clitocyboid. Hymenophoral trama regular or subregular, sometimes a mediostratum and a lateral stratum differentiated but hyphae of the lateral stratum (excepting the primordium) not divergent. Veil either entirely absent or fugacious and not glutinous. Basidia normal, but sclerobasidia often differentiated, these pseudoamyloid. Cystidia none, or very inconspicuous, hyphous or as cystidioles. Pigment

dull (gray, fuscous, cinnamon, sordid drab, at times with an olivaceous hue, never bright green, red, violet, yellow, orange), intracellular, or membranal to incrusted. Hyphae with or without clamp connections. Epicutis either hymeniform or with many broad hyphal ends (at least in young specimens), or at least in a large portion of the pileus, a trichodermium, more rarely a cutis from which, at least at the margin, recurved terminal hyphal ends rise, and then hyphae often multi-septate, not gelatinized or scarcely so. Spores not stellate, smooth with homogeneous wall, often or always binucleate in their majority. Latex none. - On soil and humus in and outside the forest, not ectomycorrhizal.

*Development of the carpophores.* Monovelangiocarpous and stipitocarpous in *H. atropunctatus*, probably also in other species, possibly gymnocarpous in some (?).

*Area:* Europe, Asia, North and South America, possibly almost cosmopolitan.

*Limits:* This genus is intermediate between *Hygrocybe* and *Camarophyllus*. It differs from the former by the structure of the epicutis, the constant absence of bright colors, and the constant habit (clitocyboid). In habit it is like *Camarophyllus*, but differs in the structure of the epicutis and hymenophoral trama. In both *Hygrocybe* and *Camarophyllus* clamp-less species are more rarely encountered than in *Hygrotrama*. The section *Tristes* of *Hygrocybe* which because of the absence of bright pigments might appear to be close to *Hygrotrama* can easily be distinguished by the habit which is more tricholomatoid, with not decurrent lamellae, often has a nitrous odor or changes color when bruised, and most species have much larger spores than the *Hygrotramas* (where they are usually smaller than 7  $\mu\text{m}$ , more rarely reaching up to 9  $\mu\text{m}$  in length); none of them has a veil. Other dull-colored species of *Camarophyllus* or *Hygrocybe* which might be confused with *Hygrotrama* have a strongly gelatinized epicutis and glutinous pileus (and often stipe).

The existence of an intermediate group between the *Camarophylli* and the *Hygrocybes* has caused some authors to combine all three genera into one (*Hygrocybe*), for instance Orton & Watling. Since they have to subdivide this large, emended *Hygrocybe* along the same lines, the decision is merely set at a lower level, and reflects the genus concept of the authors rather than their classification.

Since many species of *Hygrotrama* including the type species, have incrusting pigments rather than exclusively intracellular ones, Kühner (1979) considers the possibility of transferring *Hygrotrama* to the Tricholomataceae where it would somehow approach *Omphalina*. This brings up the question as to whether there is a clear hiatus between *Hygrotrama* and *Omphalina*. The relation of the spore length to that of the basidia is in no case of my numerous measurements in *Omphalina* reaching the proportion 1:5 whereas in *Hygrotrama* the relation is 1:5-6.5 according to my measurements with only occasional carpophores showing 1:4.8 average (for example the 4-spored *Hygrotrama tetrasporum*). Since such exceptions exist also in undoubtedly fully representative species of *Hygrocybe*, and adding the anatomical differences in pileus epicutis structure, I believe that the hiatus, considering all characters, is significant enough. This conclusion is confirmed by the fact that the few species with well known ontogenetic data available in both genera show them to

be different: Monovelangiocarpous in *Hygrotrama* (Reijnders) and gymnocarpous in *Omphalina*. Bigelow combines *Omphalina* with some other tricholomataceous genera under the generic name *Clitocybe*, and Hesler & Smith combine all hygrophoraceous genera under the name *Hygrophorus*.

Kühner, at any rate, considers "the combined *H. deceptivus* and [subgen.] *Hygrotrama*" as "certainly very natural". He leaves open the question as to whether this genus - our *Hygrotrama* - should be placed in the Hygrophoraceae. I am not aware of a study of the cultural characters of *Hygrotrama* compared with those of the other Hygrocysteae. Since the sum of the anatomical, cytological and ecological characters place the genus between *Camarophyllus* and *Hygrocybe*, it may well be expected that *Hygrotrama* shares with the latter two the difficulty (repeatedly mentioned by Kühner) one finds in growing mycelia from parts of carpophore tissue, a difficulty I can confirm as far as various agar media and *Hygrocybe* are concerned. Since such difficulties - whatever their biochemical basis - are not encountered in the comparable genera of Tricholomataceae, it might be well worth while to find out what the cultural characters of the *Hygrotramas* are.

*State of knowledge:* At present 15 species are known to belong in *Hygrotrama*.

## SPECIES

Subgenus I. **Hygrotrama**. Epicutis hymeniform, consisting of rather short elements (this hymeniform layer may occasionally be reduced to certain areas of the pileus and less distinct in others).

*Type species: H. dennisianum* Sing.

Section *Hygrotrama*. Clamp connections present.

*Type species: H. dennisianum* Sing.

*H. dennisianum* Sing.; *H. leucopus* Sing.; apparently also *H. pedicellatum* Natarajan & Menjula.

Section *Hodophilus* (Heim ex Herink) Sing. (1972). Clamp connections absent.

*Type species: H. foetens* (Phill. apud Berk. & Br.) Sing.

*H. hymenocephalum* (Sm. & Hesl.) Sing.; *H. subfuscescens* (Smith & Hesl.) Sing.; *H. foetens* (Phill. ex Berk. & Br.) Sing.; *H. atropunctum* (Pers. ex Fr.) Sing. (sensu Lange); *H. rugulosum* (Sm. & Hesl.) Sing.; apparently here according to description: *Hygrophorus phaeoxanthus* Romagnesi.

Subgenus II. **Camarophyllopsis** (Herink) Sing. (1972). Epicutis not hymeniform, merely a trichodermium, and even this often strongly reduced to recurved hyphae at the margin (and then often with a fugacious veil), or with numerous cystidiform terminal cells.

*Type species: H. schulzeri* (Bres.) Sing.

*H. schulzeri* (Bres.) Sing.; *H. rugulosoides* (Hesl. & Sm.) Sing.; *H. microsporum* (Sm. & Hesl.) Sing.; *H. paupertinum* (Sm. & Hesl.) Sing.; *H. peckianum* (Howe) Sing.; *H. deceptivum* (Sm. & Hesl.) Sing.; *H. albipes* Sing.; *H. hiemale* (Sing. & Cléménçon) Sing.; *H. tetrasporum* Sing. ined. Obviously also here according to description: *Omphalia atrovelutina* Romagnesi.

## 12. NEOHYGROPHORUS Sing.

*Lilloa* 22: 149. 1949 (publ. 1951) ex Sing., *Sydotia* 15: 46. 1961.

*Type species: Hygrophorus angelesianus* Sm. & Hesl.

*Syn.: Hygrophorus* subgenus *Pseudohygrophorus* Sm. & Hesl., *Lloydia* 5: 6. 1942.

*Characters:* Those of the preceding genus but spores amyloid; trama reddening with KOH; hymenophoral trama consisting of hyphae often larger than 7 µm in diameter (reaching 12.5 µm in diameter). On the ground.

*Development of the carpophores:* Unknown but probably gymnocarpous.

*Area:* Western North America (Olympic Mts.).

*Limits:* This genus is easily distinguishable from all other Hygrophoraceae by its amyloid spores. The author has studied the type specimens of the type species in order to be able to point out possible relations with the Tricholomataceae, especially the genus *Dermoloma*. However, this species, by virtue of its decidedly strongly elongated basidia, its viscid pileus, and the typical *Camarophyllus* lamellae does not appear to have any close affinities with non-hygrophoraceous groups. While there is a striking similarity between this species and similarly colored species of *Camarophyllus*, there is no such similarity between it and *Cantharellula* or *Porpoloma*. *Neohygrophorus* differs from *Cantharellula* as well as from the other genera near *Cantharellula* either because of the lack of incrusting pigment, or because of the characters of its lamellae or the surface of its pileus, or because of the abundance of clamp connections. *Neohygrophorus* is somewhat intermediate between *Camarophyllus* and *Hygrocybe* since its hymenophoral trama is more like that of *Hygrocybe* sect. *Coccineae* whereas its macroscopical characters are closer to *Camarophyllus*. See also under *Dermoloma*, p. 422.

*State of knowledge:* One single species is known.

*Practical importance:* None.

## SPECIES

*N. angelesianus* (Sm. & Hesl.) Sing. (*Hygrophorus*, Sm. & Hesl.).

### 13. HYGROCYBE Kummer

Führ. Pilzk., p. 26. 1871.

Type species: *H. conica* (Scop. ex Fr.) Kummer.

Syn.: *Agaricus*, trib. *Clitocybe*, subtribus *Hygrocybe* Fr., Syst. Mycol. 1: 101. 1821.

*Hygrophorus*, trib. *Hygrocybe* Fr., Epicrisis p. 329. 1838.

*Godfrinia* R. Maire, Rech. cyt. tax. Basidiomyc., p. 116. 1902.

*Hydrocybe* (ex errore), (Fr.) Karst., Bidr. Känn. Final. Nat. Folk 32: xvii. 1979\*.

*Hydrophorus* Batt. ex Earle, Bull. N. Y. Bot. Gard. 5: 431. 1909.

*Bertrandia* Heim, Rev. Myc. 1: 224. 1936.

*Gliophorus* Herink, Acta Mus. Boh. Sept. Liberec. 1: 80. 1959.

*Neohygrocybe* Herink, ibid. p. 70.

**Characters:** Those of the family; pileus viscid or dry, often bright red (near "spectrum red") or bright (lemon) yellow, often the former fading into the latter, or blending into a fire-red-orange, more rarely livid violet, green, rose color, vinaceous, etc., or with dull colors (grayish-fuscous pigments), or without any pigment; in the latter case (i.e. if with dull or no pigment) the lamellae are non-decurrent, while in the bright colored forms they are either decurrent, adnexed to subdecurrent, or adnexed to adnate-sinuate; spores pure white in print, inamyloid, uninucleate or binucleate with the wall homogenous, rarely slightly heterogenous; basidia 4-spored, or 2-spored; cystidia and/or cheilocystidia sometimes present, filamentous; hymenophoral trama subregular or regular (Pl. 27, 3) and many hyphae broader than 7  $\mu\text{m}$ ; stipe longitudinally innately striate or glassy-smooth, dry or glutinous; context mild, more rarely bitter; latex none or watery. In open fields, meadows, mountain slopes, lawns, etc., more rarely in the dense woods and tropical hammocks, rarely on wood, usually on the soil or on sand dunes, in the mud of swamps, etc., never ectomycorrhizal.

**Development of the carpophores:** Incompletely known, probably gymnocarpous at least in the majority of the species; certainly so in *H. miniata* according to Douglas, and in *H. firma* (Corner).

**Area:** Nearly cosmopolitan, from the sea shore to the alpine region, and from the arctic and subantarctic to the tropical zones.

**Limits:** There are several species which were formerly considered as *Camarophyllus* rather than *Hygrocybe*. But they all have the hymenophoral trama as in *Hygrocybe*, according to the key, and the fact that they have either binucleate spores (according to Kühner) or are closely related to species with binucleate spores and typical *Hygrocybe* colors makes the hiatus between *Camarophyllus* and *Hygrocybe* still more distinct. Furthermore, according to Kühner, the large cells of the trama of the stipe contain many nuclei whereas those of *Camarophyllus* are said to contain two to four. This is a perfectly valid differentiation for *Hygrocybe* sect. *Hygrocybe*. More data are needed in order to make it general for *Hygrocybe*.

\*Species transferred to or described in *Hydrocybe* after 1879 are here considered to have been legitimately transferred to or described in *Hygrocybe* if the intention was to describe a hygrophoraceous species rather than a cortinariaceous one.

In contrast to this, several species have been described in *Hygrocybe* that in the author's opinion do not belong in that genus, see *Humidicutis*. Recently Herink has divided the genus into three, *Hygrocybe* sensu stricto, *Neohygrocybe* and *Gliophorus*. Although at least one of these represents a well defined group within *Hygrocybe* sensu lato it is thought that generic separation is not warranted with the diagnostic characters at hand.

In section *Transformabiles* many spores are slightly punctate because of a slight heterogeneity of the spore walls and the basidia are less than 5.5 times longer than the longitudinal axis of the spores. This species is without visible affinities in the Tricholomataceae (where it might be looked for under *Fayodia*) and, in view of its similarity with other species of *Hygrocybe*, I have, for the time being, left it in this genus. It may be another example where a transition towards the Tricholomataceae is conceivable (cf. also under *Omphaliaster*).

Clampless forms exist in bisporous forms of section 3, and occasionally in collections of species of sections 6 and 7. *H. foliirubens* (type examined) is not one of them.

*State of knowledge:* Thanks to the efforts of several European authors (Kühner, Orton, Arnolds, Moser, Bon, and others) and to the studies on Western Hemisphere species by Hesler & Smith, Pegler, and others the genus *Hygrocybe* is now comparatively well known. This is, however, one of the genera where complete indications on the characters of the fresh specimens are essential because in many cases they look very different when dried, and do not reveal their bitter taste in herbarium specimens; also, the structure characteristic for viscid or glutinous surfaces on the pileus and the stipe are not always demonstrable on dried material and should be noted carefully immediately after collecting. Kühner (1977) noted that for precise specific identification it is useful to know whether the majority of the spores are uni- or binucleate. Because of the absence of some of these data, some tropical species which have been available to modern taxonomists only in dried condition, can not yet be inserted in our classification with certainty. 57 species are here enumerated.

*Practical importance:* Probably all species are edible but caution is indicated in the section *Hygrocybe*, since "*Hygrophorus conicus*" had been labeled deadly poisonous by Demange in Indochina and Josserand (1968) has mentioned as poisonous a species apparently belonging to *H. acuteconica*. Stadelmann et al. found muscarine and epimuscine in *H. nigrescens*.

## SPECIES

**Sect. 1. TRISTES** Bat. (1910). (= *Camarophyllus*, sect. *Fornicati* Bat. 1910; sect. *Ovini* Bat. 1910; sect. *Emarginatae* Lange 1923). Pigment of the pileus and lamellae not brightly colored, either practically absent, or dull colored (gray to fuscous); epicutis of the pileus not well differentiated, never formed by erect filamentous hyphae which are imbedded in a glutinous mass; stipe not truly viscid; spores

sometimes binucleate (in *H. ovina*, according to Kühner), uninucleate in *H. fornicata* (Kühner 1979); hymenophoral trama subregular.

Type species: *H. nitrata* (Pers. ex Fr.) Karst.

*H. fornicata* (Fr.) Sing. (Hygrophorus, Fr.; Camarophyllus, Karst.; *H. streptopus* Sing. & Kuthan; *H. nitrata* (Pers. ex Fr.) Karst.; *H. ammophila* Sing.; *H. cinerascens* (Berk. & Br.) Pegler; *H. nitrosa* (Blytt) Moser; *H. ovina* (Bull. ex Fr.) Kühner [Hygrophorus, Fr.; Camarophyllus, Kummer].

Sect. COCCINEAE Fayod (1889). (*Puniceae* Fayod 1880, descr. exclusa; *Pseudocamarophyllus* Sm. & Hesl. 1942; *Miniatae* Sing. 1943; *Inopodes* Sing. 1943; *Firmeae* Heinemann 1963). Edge of the lamellae homomorphous; pellicle not provided with a differentiated epicutis consisting of a layer of erect filamentous hyphae imbedded in a gelatinous mass; hymenophoral trama subregular; stipe not distinctly glutinous or viscid, sometimes innately longitudinally fibrillose-striate; subhymenium not strongly gelatinized; pigments always bright red or yellow.

Type species: *H. coccinea* (Schaeff. ex Fr.) Kummer.

Subsect. *Coccineae* (Bat.) Sing. = *Pseudocamarophyllus* subsect. *Laevi* Sm. & Hesl. 1942. Pileus smooth in wet and dry condition; stipe not longitudinally striate; lamellae adnexed, adnate, or decurrent; basidia not dimorphic (neither are spores).

Type species: *H. coccinea* (Schaeff. ex Fr.) Kummer.

*H. coccinea* (Schaeff. ex Fr.) Kummer. (Hygrophorus, Fr.); *H. quieta* (Kühner) Sing. (Hygrophorus marginatus Peck sensu Kühner non Peck; Hygrophorus quietus Kühner); *H. parvula* (Peck) Murr.; *H. mexicana* Sing.; *H. rubroflava* Sing.; *H. pumanquensis* Sing. apud Lazo; *H. striatella* Sing. apparently also *H. aurantia* Murr.; *H. blestiana* Sing.; *H. subceracea* Murr.; *H. subcaespitosa* Murr.

Subsect. *Squamulosae* (Bat. 1910 ut subsect. *Squamulosi* sectionis *Laetorum*) [= *Squamulosi* (Bat.) Konr. & Maubl. 1924-1937; sect. *Pseudoamarophyllus* subsect. *Squamulosi* (Bat.) Sm. & Hesl. 1942]. Pileus innately lacerate-squamulose, especially in the center when dry (not dried), less so, or smooth, when humid and near the margin; lamellae adnexed to adnate or decurrent; pileus usually dry (not distinctly viscid or glutinous); basidia often dimorphic.

Type species: *H. turunda* (Fr.) Karst.

*H. turunda* (Fr.) Karst. sensu Karst. (Hygrophorus, Fr.); *H. cantharellus* (Schw.) Lange (Agaricus, Schw.; Hygrophorus, Fr.; Camarophyllus, Murr.); *H. miniata* (Scop. ex Fr.) Kummer (Hygrophorus, Fr.) with several forms or varieties; *H. swanetica* Sing.; *H. batistae* Sing.; *H. paraibensis* Sing.; *H. siparia* (Berk.) Sing.; *H. firma* (Berk. & Br.) Sing.\*; *H. chilensis* Sing.; *H. lateritiorosella* Sing.

\*Not all "varieties" described by Corner and Dennis are conspecific with the type variety of *H. firma*; see Pegler, Kew Bull. 32: 297-312. 1978. In South America several additional species with di- or trimorphic basidia and spores were discovered. Since in these species the di- to tri-morphism of the basidia and spores is often the only character of any major taxonomical importance, we do not, for the time being, separate them under a special subsectional name (*Firmeae*).

Subsect. *Inopodes* (Sing. 1943 ut sectio). (= Sect. *Euhygrocybe* subsect. *Obtusae* Sm. & Hesl. 1942, pp. ?). Pileus dry or viscid and drying out rapidly, not squamulose when drying out; stipe innately longitudinally fibrillose-striate; Lamellae never decurrent.

Type species: *H. punicea* (Fr.) Kummer.

*H. punicea* (Fr.) Karst. (*Hygrophorus*, Fr., non sensu Fayod); probably also *H. marchii* (Bres.) Möller (*Hygrophorus*, Bres.) and *H. laetissima* (Sm. & Hesl.) Sing. (*Hygrophorus*, Sm. & Hesl.).

Sect. 3. *HYGROCYBE* [*Conicae* Fayod (1889) = *Laeti*, subsect. *Campanulati* Bat. 1910; *Euhygrocybe* Sm. & Hesl. max e parte, praec. subsect. *Conici* Sm. & Hesl. 1942]. Pigments bright red or yellow, pinkish vinaceous or none; pileus often glutinous; stipe often innately fibrillose-striate, or at least not glutinous in most cases; hymenophoral trama strictly regular, consisting of parallel hyphae (Pl. 27, 3); epicutis of the pileus not consisting of erect hyphae except in pilose species (e.gr. *H. erinacea*); basidia frequently of the *Godfrinia* type; context sometimes blackening, never reddening, mild to the taste; cheilocystidia usually none but (pseudo-)cystidia often present.

Subsect. *Hygrocybe* (*Conicae* Sm. & Hesl. 1943). Pileus conical at least in youth.

Type species: *H. conica* (Scop. ex Fr.) Kummer.

*H. conica* (Scop. ex Fr.) Kummer (*Hygrophorus*, Fr.; *Godfrinia*, R. Maire); *H. nigrescens* (Quél.) Kühner (*Hygrophorus*, Quél.; *Hygrocybe pseudoconica* Lange); *H. veselskyi* Sing. & Kuthan; *H. astatogala* (Heim) Heinem.; *H. singeri* (Sm. & Hesl.) Sing. (*Hygrophorus*, Sm. & Hesl.); *H. hyphaemacta* (Corner) Pegler (with dimorphic spores and basidia); *H. brevispora* Möller; *H. acuteconica* (Clem. in Woods) Sing. (*Mycena*, Clem. in Woods; *Hygrophorus*, A.H. Smith); *Hygrocybe persistens* (Britz.) Sing. (sensu Britz., Sing. & Kuthan non al; see *Zeitschr. f. Pilzk.* 42: 10. 1976.); *H. cuspidata* (Peck) Murr. (*Hygrophorus*, Peck); *H. foliirubens* Murr.; *H. spadicea* (Scop. ex Fr.) Karst.; *H. erinacea* (Pat.) Sing. (*Hygrophorus*, Pat.) - obviously also *H. apala* (Berk. & Br.) Pegler & Rayner. Perhaps also *H. calyptraeformis* (Berk. & Br.) Fayod, and, according to Kühner; *H. obrussea* (Fr.) Wünsche.

Subsect.: *Obtusae* (Sm. & Hesl. 1942). Pileus obtuse.

Type species: *H. huronensis* (Sm. & Hesl.) Sing.

*H. huronensis* (Sm. & Hesl.) Sing.\* (*Hygrophorus*, Sm. & Hesl.); *H. flavescens* (Kauffm.) Sing. (*Hygrophorus puniceus* var. *flavescens* Kauffm.; *Hygrophorus flavescens* Sm. & Hesl.).

Sect. 4. *MINUTULAE* Sing. (1973). Pigments bright; a glutinous layer on pileus and stipe present; epicutis an ixocutis. Hymenophoral trama regular to subregular

\*White forms have been observed among groups of *H. flavescens* which are indistinguishable from *H. huronensis*. The latter is therefore probably a white variety of *H. flavescens*.

(but not consisting of strictly parallel hyphae). Basidia long. Spores with one nucleus and homogeneous wall.

*Type species: H. minutula* (Peck) Murr.

*H. minutula* (Peck) Murr.; *H. nitida* (Berk. & Curt.) Murr.; *H. flavifolia* (Smith & Hesl.) Sing.; *H. ceracea* (Wulf. apud Jacq. ex Fr.) Kummer (sensu Sm. & Hesl. non Bres.); *H. chlorophana* (Fr.) Karst.; *H. reai* (Maire) Lange; *H. octayensis* Sing.; *H. subminutula* Murr.

Sect. 5. *TRANSFORMABILES* Sing. (1973). Differing from the preceding section only in relatively shorter basidia and slightly heterogeneous, alternatingly denser and less dense, spore wall.

*Type species: H. transformabilis* Sing.

*H. transformabilis* Sing.

Sect. 6. *LAETA* (Bat.) Sing. (1951) (*Hygrophorus* sect. *Laeti* Bat. 1910; *Glutinosae* Kühner 1926; *Subglutinosae* Sing. 1942 ex typo). Pigments either nearly absent or bright colored, not gray-bister-fuscous. Stipe glutinous; pileus not conic, with ixotricho dermum; cheilocystidia often present.

*Type species: H. laeta* (Pers. ex Fr.) Kummer.

*H. laeta* (Pers. ex Fr.) Kummer; *H. sciophana* (Fr.) Karst. (*Hygrophorus perplexus* Smith & Hesl.); *H. proteus* Sing.; *H. pallida* (Smith) Sing.; *H. arechavaletii* (Speg.) Sing.; *H. citrina* (Rea) Lange; probably also *H. hondurensis* Murr. and *Hygrophorus westii* Murr.

Sect. 7. *UNGUINOSAE* (Herink) Sing. Differs from the preceding section in dull colors (gray, bister, fuscous). Here and in section 6 clamp connections often scarce.

*Type and only known species: H. unguinosa* (Fr.) Karst.

#### 14. *HUMIDICUTIS* (Sing.) Sing.

*Sydotia*, 12: 225. 1957.

*Type species: Hygrophorus marginatus* Peck.

*Syn.: Tricholoma* subgenus *Humidicutis* Sing., *Sydotia* 2: 28. 1948.

*Characters:* Those of the family. Combines the presence of bright pigments with the absence of clamp connections; pileus mostly conical; lamellae neither deeply decurrent nor subfree; hymenophoral trama regular; pigment not easily dissolved in alkali solutions. Spores larger than 7  $\mu\text{m}$ . On the ground in steppes and forests.

*Development of the carpophores.* Unknown.

*Area:* North America and Northern Asia; also temperate Zone of Southern South America (e.gr. South Chile).

**Limits:** This genus differs from *Hygrocybe* in the characters of the hyphae, - absence of clamp connections - and the type of pigment (see *Sydowia* 12: 224. 1958; *Zeitschr. f. Pilzk.* 41: 37. 1975: absence of muscaflavin). It differs from the other species without clamp connections, now distributed in two genera (*Hygroaster* and *Camarophyllus*) in a combination of smooth spores, bright pigment, non-decurrent lamellae, and regular hymenophoral trama. It differs from *Tricholoma* in the less constantly and consistently emarginate-sinuate and somewhat thicker lamellae, the slightly longer basidia (in relation to the spore length) and the slightly different habit (especially the shape and length of the stipe in some extreme specimens). Altogether, the differences are not striking, and only seemed to be more so to those who knew only the bright colored *H. marginata* from the North American woods, without taking into consideration much less pigmented but very closely related species such as *H. czuica*. Nevertheless, if duly separated generically from *Hygrocybe* as it should be, this group has more natural affinity with other hygrophoraceous genera than with the Tricholomataceae and has therefore been reinstated in the former family.

*Humidicutis* differs from *Callistosporium* in the relatively longer basidia, the lack of internal pigment bodies in spores, basidia and hyphae, and the habit.

**State of knowledge:** Three species are known at present to the author.

**Practical importance:** Unknown, if any.

## SPECIES

*H. czuica* (Sing.) Sing. (*Hygrocybe*, Sing., *Tricholoma*, Sing.); *H. marginata* (Peck) Sing. (*Hygrophorus*, Peck; *Hygrocybe*, Murr.; *Tricholoma*, Sing.); with var. *olivacea* (Sm. & Hesl.) Sing. (*Hygrophorus*, Sm. & Hesl.); *H. rosella* (Speg.) Sing.

### Tribus *Hygroastreeae* Sing.

trib. nov. (Sporis nodosis vel stellatis. Typus est *Hygroaster* Sing.)

**Type genus:** *Hygroaster* Sing.

**Characters:** Spores nodose or stellate; clamp connections absent; pigments dark, not bright colored, or absent. Oleiferous hyphae numerous.

## KEY TO THE GENERA

- A. Pigment either absent or, if present, mainly vacuolar, with very sparse and faint incrusting (or inter-cellular) pigment seen in dried material; pseudocystidia none, or poorly developed; hymenophoral trama typically subbilateral with a pigmented mediostratum in pigmented species. Tropical species 15. *Hygroaster* p. 208
- A. Pigment always abundantly present, incrusting and intraparietal; pseudocystidia ± distinct; hymenophoral trama regular. Temperate, boreal and subalpine species. 16. *Omphaliaster*, p. 208

## 15. HYGROASTER Sing.

*Sydwia* 9: 370. 1955.

*Type species: Hygrophorus nodulisporus* Dennis.

*Characters:* Those of the family. Carpophores rather small to small, fresh either white or pigmented and dried becoming brownish to black; pigment mainly vacuolar where present, with or without very sparse and faint incrusting (or inter-cellular ?) pigment in dried material; pseudocystidia none; oleiferous hyphae present; hymenophoral trama regular to bilateral with the mediostratum often pigmented and the lateral stratum always hyaline, often somewhat gelatinized, hyphae inamyloid and somewhat interwoven; spores relatively large (9.5-14 µm with ornamentation), subglobose, beset with obtuse cylinders or acute spines thus appearing stellate, inamyloid, acyanophilous; basidia mostly 4-spored, about 4.8-5.8 times longer than the longer diameter of the spores (including ornamentation; up to 8.8 times longer than spores without ornamentation); epicutis - a cutis of smooth filamentous hyphae. Pileus subumbilicate or umbilicate; lamellae adnate to adnate-subdecurrent, subdistant or distant, thickish; stipe (as pileus) not gelatinized, narrowly hollow, not insititious. Odor none. On earth in neotropical forests.

*Development of the carpophores:* Not known in detail, probably gymnocarpous.

*Area:* From Trinidad to Amazonia.

*Limits:* The size and shape of the spores are shared only with *Omphaliaster* as far as genera of Hygrophoraceae are concerned, and can be compared with those of *Laccaria*. The latter genus and its relationships are discussed on p. 233. *Asproinocybe* has similar but much smaller spores and conspicuous laticifers.

*State of knowledge:* Two species are well known.

*Practical importance:* Unknown.

### SPECIES

*H. nodulisporus* (Dennis) Sing.; *H. albillus* Sing.

## 16. OMPHALIASTER Lamourc

*Svensk Bot. Tidskr.* 65: 281. 1971.

*Type species: Rhodocybe borealis* M. Lange & Skifte

*Characters:* Those of the preceding genus but differing mainly in pigment topography, see key above.

*Development of the carpophores:* Probably as in *Hygroaster*.

**Area:** North-temperate to boreal.

**Limits:** The genus is so close to the preceding one that it was originally not recognized to be different (Singer 1975). However, with some hesitation, based on the fact that even with the addition of a further species in *Hygroaster*, the limits between the two genera seem to remain intact and the area of distribution appears to be discontinuous, the genus is now recognized. Nevertheless, the clearly hygrophoraceous position of *Hygroaster* make it impossible to transfer *Omphaliaster* to the Tricholomataceae as has been suggested. Lamoure states (translation from the Latin): “[*Omphaliaster*] differs from the Hygroasters whose clampless hyphae it has, in not colored cell sap and therefore is not related to the Hygrophori.” Since other Hygrophoraceae do indeed have colorless cell sap and even intraparietal (“membranal”) and incrusting pigments, for example some *Hygrotrama* species, Lamoure’s statement does not carry much weight if the term “Hygrophori” is meant to refer to the Hygrophoraceae in general. The basidial characters are important in this regard only if taken with reference to spore size. According to my own measurements on *O. asterophorus* they are  $(33)-42.5-58.5 \times 9-11 \mu\text{m}$  and thus would be about 5.2 times longer in an average than the spore length, much more so if the sporoid (without ornamentation) is measured. Even if other measurements were also correct, this would not be the only case of exceptional basidial length in species which otherwise obviously belong in an hygrophoraceous genus, for example *Hygrocybe* (e.gr. *H. transformabilis*). In such cases, the general affinity of the respective taxon has to be taken into consideration and there is no doubt that *Omphaliaster* is much more closely related to *Hygroaster* than to *Omphalina*.

Baroni (1981) has shown that *Rhodocybe ianthinocystis* Sing. is not a *Rhodocybe*. He believed that the species belongs in *Omphaliaster*. However, the much smaller and much less strongly ornamented spores, the (fresh) strongly pigmented (the pigment is amethyst color) laticifers, non-incrusted hyphae, and the geographical location of the species (as well as the presence of clamp connections if Baroni’s observation is correct) make this proposal unacceptable. This species belongs in the genus *Asproinocybe* Heim (Tricholomataceae) inasmuch as the basidia are short ( $16.5-20 \times 5.3-6.2 \mu\text{m}$ , i.e. less than 5 times the length of the spore length).

**State of knowledge:** Two species are well known.

**Practical importance:** None as far as known.

## SPECIES

*O. borealis* (M. Lange & Skifte) Lamoure; *O. asterosporus* (Lange) Lamoure

## TRICHOLOMATACEAE Roze

(ut Tricholomées), *Bull. Soc. Bot. Fr.* 23: 51. 1876, nom. nud.; *ibid.* p. 112. 1876; Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 19. 1927; Heim (ut Tricholomaceae), *Treb. Mus. Ciènc. Nat. Barcelona* 15: 86. 1934; Singer, *Ann. Mycol.* 34: 328. 1936.

- Syn.: *Mycenaceae* Roze, l.c., p. 51 and 109 (ut Mycenées); Van Overeem in Van Ov. & Weese, *Ic. Fung. Malayens.* 14-15: 4. 1926.  
*Marasmiaceae* Roze, l.c., p. 51 and 108 (ut Marasmiées); Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 13. 1927. Roze ex Kühn, *Bull. Soc. Linn. Lyon* 49: 16. 1980.  
*Clitocybaceae* Roze, l.c., p. 51 and 112 (ut Clitocybées); Van Overeem, l.c., p. 21.  
*Omphaliées* Roze, l.c., p. 108.  
*Collybiées* Roze, l.c., p. 109.  
*Armillariacées* Roze, l.c., p. 113.  
*Agaricacei* Schroeter in Cohn, *Krypt. Fl. Schles.*, *Pilze* 3 (1): 519. 1888 (non *Agaricei* Fr.).  
*Lachnellaceae* Boudier, *Hist. Classif. Discomyc.* p. 118. 1907.  
*Cyphellaceae* Lotsy, *Vortr. Bot. Stammesg.* 1: 696-698. 1907\*.  
*Eoagaricaceae* Krieger, *Bull. Md. Acad. Sc.* 3: 8. 1923.  
*Dictyolaceae* Gäumann, *Vergl. Morph. Pilze* p. 511. 1926 (quoad typum).  
*Leptotaceae* Maire, *Publ. Junta Cienc. Nat. Barcelona* 120: 52. 1933, nom. nud.  
*Physalacriaceae* Corner, *Beih. Nov. Hedw.* 33: 10. 1970.  
*Amparoinaceae* Sing. *Rev. Mycol.* 40: 58. 1976.  
*Dermolomataceae* (Bon) Bon, *Docum. Mycol.* 9(35): 43. 1979.  
*Macrocytidiaceae* Kühn., *Bull. Soc. Linn. Lyon* 48: 172. 1979.  
*Rhodotaceae* Kühn, l.c. 49:235. 1980.  
*Laccariaceae* Jülich, *High. Taxa Basid.* p. 374. 1981.  
*Lyophyllaceae* Jülich, l.c. p. 378.  
*Nyctlidaceae* Jülich, l.c., p. 381.  
*Termitomyctaceae* Jülich, l.c. 391.  
*Leucopaxillaceae* Jülich, l.c., p. 376.  
*Biannulariaceae* Jülich, l.c., p. 356.  
*Resupinataceae* Jülich, l.c., p. 388.  
*Panellaceae* Jülich, l.c., p. 382.  
*Fayodiaceae* Jülich, l.c., p. 367.

Type genus: *Tricholoma* (Fr.) Quéel.

**Characters:** Carpophores not combining bilateral hymenophoral trama with inamyloid spores and adnato-decurrent or free lamellae; not combining elongate (more than 5.5 times longer than the spores) basidia without carminophilous granulation with simple, non-crowded lamellae; not combining blackening laticifers and basidia and spores with the presence of a watery latex and inamyloid spores. Pileus and stipe never both covered with a thick epithelium. Stipe never with a cortina that is attached to the margin of a marginate bulb. - Lamellae sometimes free or subfree, or concurrent, adnexed, adnate, sinuate, or decurrent (if the lamellae are free or subfree, the spores are uninucleate at the time of discharge); hymenophoral trama intermixed, irregular, subregular or regular (rarely bilateral and then spores uninucleate) never inverse; spores in spore print pure white, cream color, light creamy pink, pale violet, light greenish, or pale sordid grayish, never deep or bright colored; wall simple, or heterogeneous (and then spore print pure white), simple or

\*Unless Roze's form of publishing family names is considered valid, the name of the present family would become Cyphellaceae or Lachnellaceae (if types included in the Agaricales, see p. 16), Eoagaricaceae or Dictyolaceae (if not). All these alternatives are undesirable to a degree that the conservation of Tricholomataceae would have to be proposed (which has not been done at the time of this writing). An alternative would be the acceptance of a rule that would, for fungi, authorize the use of "pseudo-vernacular" family names. The latter solution would be preferable since it would avoid conserved family names in the fungi and would, at the same time, take care of similar cases e.g. Cortinariaceae. (see *Taxon* 33: 764, prop 43. 1984)

more rarely complex (i.e. rarely well differentiated into endo-, epi-, and exosporium), without a germ pore, inamyloid, amyloid, or rarely pseudoamyloid (and then frequently also with pseudoamyloid hairs on the pileus); basidia sometimes of the *Lyophyllum*-type (tribus *Lyophylleae*) i.e. with carminophilous granulation; sterigmata (1)-2-(3)-4; cystidia or pseudocystidia present or absent; stipe central or eccentric, or lateral, or absent, never with a truly basal volva in mature specimens, rarely with latex (*Mycena* p.p., *Lactocollybia* p.p.); with amyloid, pseudoamyloid or inamyloid, partly gelatinized or nongelatinous trama, its hyphae with thin or thick walls, homoiomeric, sometimes with separation zones between the pileus and the stipe, the latter, if present, fleshy, cartilaginous or chordaceous, with or without a fibrillose-lacerate basis (from the basal tomentum). Hyphal system monomitic (including "sarcodimitic" but never amphimitic nor trimitic and generally not dimitic\*).

Taste mild, bitter, or acrid. On the ground in woods and on all kinds of decaying substrata (most frequently), also on living hosts (Russulaceae, and Cormophyta of various families), in deep moss, on charcoal, on earth, sand, and peat in meadows, fields, on lawns, in bogs, gardens, deserts, steppes, tundras and prairies, marshes, etc.

**Limits:** The limits of this family have been discussed in the Hygrophoraceae (p. 191) and Polyporaceae (p. 164). They are also discussed regarding the Crepidotaceae, Paxillaceae, Cortinariaceae, Agaricaceae, Amanitaceae and Entolomataceae (see the genera concerned).

This is the largest family of the Agaricales, and it has been attempted to subdivide it into smaller families. It is perhaps possible to divide it into two families, Tricholomataceae sensu stricto, and Mycenaceae Roze, Van Overeem, or in three, adding Lyophyllaceae, but such readjustments are premature.

The delimitation of the Tricholomataceae had to be clarified at another level, viz. the separating line between the Agaricales and such genera as *Rhodoarrhenia* and *Favolaschia*. As for the discussion of this problem, the reader is referred to these genera on one hand and to the chapter on phylogenetic theories in the introduction on the other.

#### KEY TO THE TRIBUS

- A. Basidia with siderophilous granulation (excluding the micro- and gigas-type); spores ± cyanophilous, hilum mostly of the open-pore type.
- B. Clamp connections absent; spore print dirty pink to dull red; mostly termitophilous, tropical species.  
Termitomycteae, p. 225

\*Corner describes a few species which, according to some of their characteristics, do not key out with the Polyporaceae, Russulaceae and the Bondarzewiaceae - the only Agaricales families where dimitic trama has been observed by the present author. These species of Corner's are unknown to me, and if taken at face value, would suggest that there are, also among some genera of Tricholomataceae, a few species with at least partly or eventually dimitic hyphal system. If this is confirmed, the affinity of Polyporaceae and Tricholomataceae would be further underscored and their separation into two orders made even less plausible. See also under *Lentinus* (p. 165, 186).

B. Clamp connections present and/or spore print white to yellowish cream; mostly non-termitophilous, subtropical and temperate species. *Lyophylleae*, p. 215

- A. Basidia not distinctly (light microscopy!) siderophilous; spores cyanophilous or not.
- C. Reduced series: Lamellae formed only exceptionally; carpophores small, with mainly smooth hymenial surface, often cypelloid.
- D. Sterile surface layer not much differentiated (without characteristic surface hairs or dermatocystidia); no *Rameales*-structure; hyphae without clamp connections; pigment absent. Bryogenous (see *Tricholomataceae*, reduced series).
- D. Not combining these characters.
- E. Trama with a gelatinized zone or completely gelatinized; without hymeniform-epicutis, but a *Rameales*-structure sometimes present (See *Resupinateae*)
- E. Trama not gelatinized, or with strongly differentiated surface structure (hymeniform, with dermatocystidia etc.).
- F. Carpophore a stipitate hollow head with pseudocystidia and basidia forming an external hymenium, or sterile surface formed by a hymeniform structure or by characteristic surface hairs which may be pseudoamyloid or partly pseudoamyloid, not cystidioid and subcapitate to capitate. Hyphae of the trama not or scarcely inflated. (See *Marasmieae*)
- F. Carpophores not consisting of a stipitate hollow head, and sterile surface not with long, characteristic hairs.
- G. Sterile surface a *Rameales*-structure (frequently strongly reduced); not with capitate or subcapitate dermatocystidia; hyphae of the trama not voluminous or inflated. (See *Collybieae*)
- G. Sterile surface with capitate or subcapitate dermatocystidia (but never hymeniform), the dermatocystidia thin-walled; hyphae of the trama all or in part inflated or voluminous. (See *Myceneae*)
- C. Hymenophore well developed, constantly venose, lamellate, or tubular.
- H. Habit collybioid; spores binucleate, inamyloid, acyanophilic, smooth; pileus often viscid, with dermatocystidia; lamellae usually yellowish; hypodermium and/or part of the hymenophoral trama ± gelatinized; stipe often vellereous, not insititious, pigmented; hyphae of the monomitic trama inamyloid, with clamp connections; mostly on wood (see "O" below)
- H. Not combining these characteristics.
- I. Strictly lignicolous species, spores with subglobose and/or cyanophilous and/or carminophilous, smooth wall, the spores usually short, mostly subglobose and the habit ± pleurotoid, fleshy. Spores and tramal hyphae inamyloid.
- J. Carpophores luminescent, containing a poisonous substance; with or without veil (see *Paxillaceae*)
- J. Carpophores non-luminescent, not containing poisonous substances (see "B" above)
- I. Fungi, if growing on wood, not combining the characters indicated above.
- K. Spore print amethyst-livid and spores smooth; stipe usually strongly reduced. Subtropical and tropical species (see *Polyporaceae*)
- K. Spore print, if amethyst colored consisting of strongly spinose-echinate spores and carpophores not lignicolous, centrally stipitate.
- L. Habit clitocyboid, omphalioid, tricholomatoid, rarely collybioid or pleurotoid; spores smooth, spirose, or finely verruculose, inamyloid; epicutis of pileus dense or in form of a cutis, not a *Rameales*-structure, with smooth hyphae, rarely trichodermal, without a gelatinous layer underneath; if epicutis contains swollen hyphal ends, these do not or only exceptionally form a hymeniform layer (*Clitocybe* sg. *Cystoclitus*), and if dermatocystidia are present, these are not numerous or strongly differentiated unless they are pseudocystidioid (dermatopseudocystidia as gloeocystidia or terminal cells of the laticiferous system); pigments not greening in KOH medium either in pileus or in stipe; trama inamyloid, lacking very long and broad hyphal cells (i.e. not "sarcodimitic"); not reviving when remoistened; hymenophoral trama regular or subregular, sometimes regular of the *Clitocybe*-type, not bilateral and basically axially oriented even if seemingly irregular (omphalioid species with very strongly inflated hypodermial or very thin often pigmented

L. Not combining the characters indicated above.

- M. Hymenophoral trama tending to remain bilateral\* for a long time; either with double veil and amyloid spores or without a distinct veil and amyloid or inamyloid spores; in the first case clitocyboid or tricholomatoid, in the second case mycenoid, collybioid, or pleurotoid; spores smooth unless carpophores ± pleurotoid and spore print pinkish.  
N. Fleshy fungi with amyloid, smooth spores. Biannulariaeae, p. 302  
N. Carpophores either not fleshy, or with inamyloid or asperulate spores.  
O. Spores asperulate, pinkish in print; habit pluteoid-pleurotoid. Growing on wood Rhodotaeae, p. 441  
O. Spores strictly smooth; spore print not pinkish; habit mycenoid or collybioid; lignicolous or not lignicolous. Pseudohiatuleae, p. 433  
M. Hymenophoral trama regular in youth (although divergent in the primordia)  
P. Spores amyloid with strictly smooth and homogeneous wall.  
Q. Hymenophore tubular or lamellate; habit pleurotoid; uppermost layer of the pileus gelatinized and/or with a *Rameales*-structure or with numerous dermatocystidia with ramifications; also a subhypodermial layer often strongly gelatinized; tramal hyphae inamyloid; cystidia often present. Panelleae, p. 346  
Q. Fungi, if pleurotoid, not with tubular hymenophore. If hymenophore lamellate, not combining the characteristics indicated above.  
R. Carpophore tricholomatoid, clitocyboid, collybioid, more rarely pleurotoid (and then fleshy, with undifferentiated epicutis hyphae, with cheilocystidia which are smooth and entire), without diverticulate hyphae or cheilocystidia, without long and broad tramal elements ("sarcodimitic" structure); dermatocystidia on the pileus, if present, not forming a discontinuous layer in the marginal half of the pileus (rather fibrils in the depressed center of the pileus) and not forming a continuous layer in the center of the pileus, epicutis, if cutis-like, not formed by very narrow hyphae with vacuolar pigment nor forming a hymeniform layer; base of neither insititious nor with a pigmented (yellow or tawny) basal tomentum; hymenophore lamellate. Leucopaxilleae, p. 287  
R. Carpophores mostly mycenoid or omphaloid, otherwise not combining the characters indicated above. Myceneae, p. 389  
P. Spores amyloid or inamyloid; if amyloid, they have not simple, homogeneous, thin wall or they have a contrasting (in Melzer's reagent) amyaceous punctuation, verrucosity or echinulate ornamentation.  
S. Spores amyloid.  
T. Carpophores omphaloid; outermost spore wall smooth or minutely and distantly spinulose; ornamentation often of type XI (light microscopy); hyphae with clamp connections (see Myceneae)  
T. Carpophores not omphaloid; outermost spore layer broken up to form a finely to coarsely verrucose or spinulose ornamentation, type

\*The bilaterality of the hymenophoral trama is often inconstant or easily overlooked. Species with apparently regular trama and a double veil, with amyloid spores, forming ectomycorrhiza, should be carefully compared with the Biannulariaeae; those with inamyloid spores, no veil and no ectomycorrhiza formation, if collybioid or "marasmoid" may have velutinous-tomentose stipe and viscid pileus and conform with the characters indicated for *Flammulina* (p. 435); in this case they should be referred to the Pseudohiatuleae. Or else, they may have flocculose to soft-spinulose yellow, brown, orange, olive, or red pileus and/or stipe and conform with the generic description of *Cryptotrama*; in this case, they also belong in the Pseudohiatuleae. They might also have a deep maroon-violet-brown pileus with the pigment dissolving to a violet solution in KOH. In this case, the fungus is also referable to Pseudohiatuleae.

II-IV, III, or mostly IV, V, VI, which is sometimes covered by an inconspicuous inamyloid perispore; hyphae with or without clamp connections (see *Leucopaxillae*).

- S. Spores inamyloid.
- U. Trama with conspicuous gloeo-vessels and/or laticiferous hyphae; epicutis not hymeniform or with *Rameales*-structure; gloecystidia often present; spore print cinnamon-pink or white to pale cream; clamp connections absent or present; carpophores collybioid or omphaliod, not reviving when remoistened; spore wall thin or thickish and double, smooth or nodulose (see *Tricholomataceae*, *Omphalinaceae*).
  - U. Trama with rather inconspicuous oleiferous hyphae.
  - V. Epicutis of the pileus mostly hymeniform, more rarely not hymeniform and then formed by broom cells (but then stipe always dark and horse-hair-like, setaceous and/or its hyphae pseudoamyloid, its surface never covered by dermatocystidia, *Rameales*-structures, or thick-walled hairs), or by pseudo-amyloid (rarely amyloid) thick-walled hairs or apical pseudo-amyloid flagella-like appendages, or by long, weakly pseudo-amyloid or inamyloid hairs which are roughened or covered by crystals (but then fungi cyphelloid without hymenophore); trama inamyloid or pseudoamyloid; spores smooth, rough or spinose, always smooth if epicutis not hymeniform carpophores mostly collybioid or pleurotoid, often reviving after remoistening; without gelatinous layers, unless epicutis hymeniform.
- Marasmieae*, p. 351
- V. Epicutis not entirely covered by a hymeniform layer (rarely with subhymeniformly arranged pigmented dermatocystidia in the middle of the pileus only, or with dermatocystidia not forming a continuous hymeniform layer, with vacuolar rarely incrusting pigment all over the pileus), nor with long pseudoamyloid hairs or elements with pseudoamyloid flagelliform appendages; trama not pseudoamyloid (unless habit mycenoid); spores smooth or asperulate to nodulose; collybioid, pleurotoid, omphaliod, mycenoid, with or without gelatinous layers in the epicutis, hypodermium, or trama.
  - W. Entire carpophore fresh entirely white (or with slight ochre discolorations) and mycenoid to omphaliod, rarely pleurotoid or trama of voluminous, broad elements (*Mycena*-structure), or trama pseudoamyloid or epicutis with diverticulate hyphae in a cutis or ixotrichodermium; trama without gelatinous layer; stipe not insititious or with basal disc; epicutis often with numerous dermatocystidia but these not forming a continuous hymeniform layer.
  - X. Epicutis with diverticulated hyphae spores not smooth. (see *Myceneae*)
  - X. Epicutis with or without diverticulated hyphae; spores smooth (see *Marasmieae*)
  - W. Not combining the characters or alternatives indicated above.
  - Y. Spores asperulate, nodulose, or punctate or hyphae of the epicutis very thin and partially filled by a vacuolar pigment, or else with numerous dermatocystidia which are in places bundled together but do not form a continuous hymeniform layer, and are often filled with a vacuolar pigment; habit mycenoid, collybioid, omphalio-

id, rarely almost clitocyboid or almost pluteoid; not revivescent, never cyphelloid, nor insititious (see *Myceneae*)

- Y. Spores smooth or asperulate or with an abaxial bulge (and then at times triangular) but usually with even outline, inamyloid, more rarely pseudoamyloid; dermatocystidia of the pileus present (and then often as terminal cells of a *Rameales*-structure) or absent, not with vacuolar pigment; habit collybioid to omphaliod or pleurotoid, sometimes revivescent, sometimes cyphelloid; stipe insititious or with basal mycelium; basidioles narrowly clavate to subcylindrical or fusoid.
- Z. Carpophores, if pleurotoid, not with typical metuloids and not with (fresh) gray or blackish lamellae; but often with pigment greening in KOH; there is frequently a gelatinous upper layer in the trama of the pileus but if so there is an eccentric or lateral stipe present; spores often with an abaxial bulge and sometimes even triangular or cruciform but wall smooth; if gelatinous zone absent, metuloids with intraparietal pigmentation and metuloids with crystalline murication absent; cheilocystidia often developed, versiform; hyphae with clamp connections or without them; lamellae often intervenose or even favoloid-connexed; spores not asperulate. *Collybieae*, p. 305
- Z. Carpophores mostly strictly pleurotoid, sometimes astipitate or with pseudostipe, or spatuloid; rarely omphaliod; a gelatinous zone in the trama of the pileus mostly present; if carpophore is not pleurotoid, metuloids with intraparietal pigment conspicuous or a distinct gelatinized zone in the trama of the pileus present; spores smooth or asperulate; clamp connections present; cheilocystidia usually present, usually rather small, often fusoid; pigment of the hyphae of the stipe not greening in KOH

*Resupinateae*, p. 338

### Tribus *Lyophylleae* Kühner

*Bull. mens. Soc. Linn. Lyon* 7: 204. 1938.

Type genus: *Lyophyllum* Karst.

**Characters:** Those of the family; basidia of the *Lyophyllum* type, i.e. with siderophilous granulation in the mature basidia (Pl. 9); spore print white to pale cream, spore powder formed of chlamydospores often brownish (where present); spores (Pl. 45; 46, 4) smooth or asperulate to echinate, inamyloid, carminophilous, cyanophilous; hyphae all inamyloid, with clamp connections, also sometimes without clamps (*Lyophyllum incarnatobrunneum* Gerhardt); cuticle usually not well differentiated, often hygrophanous, but sometimes, especially in species with bright colored cuticle, provided with a distinct epicutis consisting of small sphaerocysts; pigment incrusting the hyphal walls, or intracellular. On the soil, charcoal, on

trunks and stumps, and on dead leaves, saprophytically, also on carpophores of Russulaceae and perhaps other Agaricales, parasitically.

#### KEY TO THE GENERA

- A. Fungi growing saprophytically or, if parasitically, on living trees and then not forming chlamydospores on the surface layer of the pileus.
  - B. Stipe ± central, on earth or humus or decaying plant material; basidia with dense and distinct siderophilous granulation.
    - C. Pigment dull colored, gray, fuscous, umber, more rarely tending to ochraceous, melleous, fawn color, lilac, etc., or without pigment (but then with smooth spores, without veil and cespitose, more rarely solitary, summer- and fall-fruiting); carpophores sometimes staining yellow, blue, black or red; pigments thinly incrusting; habit tricholomatoid, clitocyboid, collybioid.
      - 17. *Lyophyllum* p. 216
    - C. Pigment dull colored as above or brighter yellow, brown, blue, lilac-violet, rarely red, sometimes absent; carpophores generally not staining or very slightly darkening; pigments vacuolar, intracellular-dissolved, or absent, not incrusting the hyphal wall. Habit tricholomatoid.
      - 18. *Calocybe* p. 221
  - B. Stipe distinctly eccentric, or if almost or quite central, rising from standing, living trees or from freshly fallen or felled trees, mostly Dicotyledones, always lignicolous; basidia siderophilous of the *Oligo*-type, and siderophily not constant in all mature basidia, sometimes absent in not fully mature specimens.
    - 20. *Hypsizygus* p. 224
- A. Fungi growing parasitically on decaying or freshly invaded Russulineae (possibly also other Agaricales); chlamydospores numerous on the surface of the pileus.
  - 19. *Asterophora* p. 222

### 17. LYOPHYLLUM Karst.

*Acta Fl. Faun. Fenn.* 2: 3. 1881, em.

Type species: *Lyophyllum leucophaeatum* (Karst.) Karst.

Syn.: *Tephrocybe* Donk, *Nov. Hedw. Beih.* 5: 284. 1962.

*Caesposus* Nüesch, *Jahrb. St. Gall. Nat.-wiss. Ges.* 68: 109. 1937 (invalid)

**Characters:** Those of the tribus. Pileus often hygrophanous, not glutinous, but often somewhat silky or opimus, smooth uneven, or striate, pigments at least partly and thinly incrusting the hyphal walls, dull colored: gray, grayish fuscous, bister, umber, more rarely tending to melleous, ochraceous or lilac, rarely absent (and then carpophores cespitose, evelate, and with smooth spores, summer-fall-fruiting); carpophores entirely or in parts frequently staining yellow, red, blue, or black. Spores globose or subglobose, ellipsoid, fusoid, ovoid, oblong, also somewhat angular with flattened sides, or tetrahedric, rhomboid, even somewhat cross-shaped) but more frequently terete, smooth, asperulate or finely spinulose, cyanophilous, carminophilous, inamyloid, typically uninucleate, but sometimes some binucleate ones intermixed, hilum of the open-pore type (Pegler & Young). Spore print pure white to cream white (between Ia and Ib of Romagnesi's chart), not dirty pink, under oil immersion hyaline, rarely with a vague fuscidulous shade, not stramineous or pinkish. Habit of the carpophores very variable, from (almost mycenoid to) collybioid, or clitocyboid to tricholomatoid. Basidia siderophilous, mostly with rather numerous relatively dense granules, at least in the fully mature

basidia, mostly 4-spored; basidioles not fusiform. Cystidia rarely present and then very inconspicuous, basidiole-shaped or hyphous. Tramal hyphae not transformed into a mass of pulveraceous chlamydospores, but chlamydospores may occur in mycelial cultures. Veil none. Saprophytically on the ground, also often on charcoal, among mosses including *Sphagnum*, rarely on rotten wood and among dead leaves. Some species perhaps facultatively ectomycorrhizal.

*Development of the carpophores:* Probably always gymnocarpous, stipitocarpous (Watling for *L. connatum*).

*Area:* Fewer species in the tropics and subtropics than in the boreal, temperate, and arid regions, but occurring in all continents excepting the Antarctica.

*Limits:* The genus was first (after Karsten who considered it related to *Paxillus*) taken up by Singer in the present circumscription (but including some species which do not belong here) in 1936; later it was more precisely delimited by Kühner who discovered the "carminophilous" granulation of the basidia. Kühner & Romagnesi include *Calocybe* in *Lyophyllum*. Orton, Donk, and Moser (1967) recognize three genera whereby Orton combines *Tephrocybe* with *Collybia*. In spite of the often collybioid habit, the subgenus *Tephrophana* (= genus *Tephrocybe*) is by no means related to or even similar to the Collybias. As far as *Tephrocybe* is concerned, Kühner & Romagnesi say correctly that "it might seem shocking to reunite under one and the same generic name species which are at first view as different as *L. aggregatum* [decastes], *atratum* and *georgii*. But when one considers other assemblages [of species] unanimously considered as natural, one often finds morphological variations of the same amplitude: *Entoloma lividum* is related to *Eccelia rhodocylix*, *Phlegmacium caerulescens* to *Hydrocybe acuta*. Clearly, if one combines the former in the same genus *Rhodophyllus* [*Entoloma*] and the latter in the same genus *Cortinarius*, as one does nowadays, one must just as well put the Tephrophanae... in the genus *Lyophyllum*."

As for *Tephrophana* (*Tephrocybe*), some species have been discovered which make the limits between that group and the rest of the *Lyophyllum* break down. Kühner & Romagnesi distinguish this section by the dull colors, thinner stipe, often striate and ± hygrophanous pileus which is not larger than 50 mm, and the context of the pileus which is never white in humid condition. Yet, some species otherwise fully like *Lyophyllum* sect. *Lyophyllum* or sect. *Difformia* have pigmented parts in the pileus trama; others, fully agreeing and related with *Tephrophana* have pallid context. An American carbonicolous species is fleshier than the other carbonicolous species and has white (inside and outside) stipe. Intermediate species are in particular: *L. fibrillosum* (Sing.) Sing. (collybioid, not hygrophanous, with pallid pileus-context); *L. semiustum* Sing. (with estriate margin and white context, otherwise like *L. anthracophilum*).

On the other hand, I believe that there is a good basis for recognizing *Calocybe* as a genus different from *Lyophyllum*. The differences in pigmentation (color as well as pigment localization) are evident and sharp as far as my experience goes, and the two genera can be easily distinguished by the characters emphasized in the key.

*Lyophyllum* has been emended so as to accommodate also species without clamp connections (see p. 220).

With regard to the affinity, presumed or otherwise, between the Lyophylleae and the Entolomataceae, see also under the latter family.

*Lyophyllum* differs sharply from *Clitocybe* (and all other tribus of the Tricholomataceae except Termitomyceteae) by the siderophilous granulation other than the micro-type. *Lyophyllum connatum* is said to have no "carminophilous" granulation or to lose it in older basidia. The species which I have collected and other collections from the Alps are obviously and persistently provided with a siderophilous granulation and a characteristic violet FeSO<sub>4</sub> reaction of the lamellae. I know of no species of *Lyophyllum* which is intermediate or inconstant in this regard. It is however possible that some species of *Clitocybe*, externally similar, has been mistaken for this *Lyophyllum*. *Lyophyllum* differs also from the genera of other tribus of the Tricholomataceae (except Termitomyceteae) by the spore hilum of the open-pore type (Pl. 45, 5).

*State of knowledge:* The genus is in need of revision by a monographer. Some species are well known, enough to establish a well founded classification of the genus. However, certain groups are not completely studied as to the delimitation of their species, a task that is complicated by the fact that, in some of these groups, the synonymy has reached such vast proportions that it seems almost impossible to attribute the right name to the right species. The following account of the 40 species known to belong in this genus, is the best that could be given without more detailed monographic studies. Such a study might well, as stated by Cléménçon (*Mycotaxon* 18: 380. 1983), lead to a revision of the limits and definition of the sections *Diformia*, *Tephrophana*, and *Lyophyllum*.

*Practical importance:* All known species are edible, some are of great local importance, and are constantly sold in the markets of Europe and Mexico.

## SPECIES

Subgen. *Lyophyllum*. Clamp connections present.

Sect. 1. *DIFFORMIA* (Fr.) Kühner (1938). Habit of the carpophores tricholomatoid or clitocyboid, mostly characteristically conglobate, even connate at the bases, thus forming large masses of compound carpophores; pilei and stipes rather thick and fleshy; context unchanging; spores globose, ellipsoid, smooth; stipe usually broader than 5 mm; on the soil.

*Type species:* *L. aggregatum* (Schaeff. ex Secr.) Kühner [= *L. decastes* (Fr. ex Fr.) Sing.]

*L. connatum* (Schum. ex Fr.) Sing. (*Clitocybe*, Gill.); *L. decastes* (Fr. ex Fr.) Sing. [*Clitocybe*, Kummer; *L. aggregatum* (Schaeff. ex Secr.) Kühner; *Clitocybe*, Gillet; *Tricholoma*, Cost. & Duf.]; *L. fumosum* (Pers. ex Fr.) Kühner & Rom. ex Orton; *L. loricatum* (Fr.) Kühner; *L. tucumanense* Sing.; *L. multiforme* (Peck) Bigelow

(*Clitocybe*, Peck). Several American species, *C. elephantina* Murr., *C. tenebricosa* Murr., *Melanoleuca submulticeps* Murr., *C. virgata* A.H. Sm.) are very closely related to *L. decastes*, possibly identical according to Bigelow. Apparently also *L. umbriniceps* (Murr.) Bigelow.

Sect. 2. *TEPHROPHANA* (Fr.) Sing. (1943). (*Collybia*, sect. *Hemicollybia* G. Beck 1922). Habit collybioid, mostly gregarious with usually rather thin pileus and stipe (but sometimes thick and fleshy), the latter hollow or becoming so in most species, often subcartilaginous, rarely broader than 5 mm, central, rarely eccentric and then not growing on wood, but often growing on or between mosses, on sand, on very decayed wood, on charcoal, or on forest soil, in the latter case sometimes with pseudorrhiza; context not blackening nor bluing; spores globose or ellipsoid.

Type species: *L. atratum* (Fr.) Sing.

Subsection *Orbisporina* Sing. (1943). Spores globose or virtually so, sometimes spinulose or verruculose.

Type species: *L. ambustum* (Fr.) Sing. (sensu Ricken = *Collybia gibberosa* J. Schäffer).

*L. gibberosum* (J. Schäffer) M. Lange; *L. anthracophilum* (Lasch) M. Lange & Sivertsen (*L. carbonarium* (Velen.) Moser in Gams); *L. sphaerosporum* Kühner & Romagnesi (differing from the preceding species in ornamented spores); *L. nodulosporum* Sing.; *L. semiustum* Sing.; *L. tylicolor* (Fr.) M. Lange & Sivertsen; possibly identical with the preceding species: *L. tesquorum* (Fr.) Sing. (sensu Lange, Kühner) and *Collybia olympiana* A.H. Smith.

Subsection *Ellipoideosporina* Sing. (1943). Spores ellipsoid.

*L. palustre* (Peck) Sing.; *L. atratum* (Fr.) Sing.; *L. rancidum* (Fr.) Sing. (*Agaricus leptorhizus* Pers.); *L. ozes* (Fr.) Sing.; *L. putidum* (Fr.) Sing.; *L. coracinum* (Fr.) Sing. (sensu Bres., Konr. & Maubl.); *L. inolens* (Fr.) Sing.; *L. mephiticum* (Fr.) Sing.; *L. langei* Sing.; *L. miserum* (Fr.) Sing.; *L. striaepileum* (Fr.) Kühner & Romagnesi (sensu Lange); *L. polyphagum* Sing. ined. Also *L. fibrillosum* (Sing.) Sing. (cn. = *Calocybe fibrillosa* Sing. *Lilloa* 25: 19. 1951).

Sect. 5. *HETEROSPORA* (Sing.) Sing. (1973). Combining tricholomatoid habit and bitter taste or uneven and/or rough spores. This section differs from Sect. 1 also in the solitary or gregarious, not cespitose growth, and stipes not connate, but more than 5 mm broad. Tropical and subtropical species.

Type species: *L. heterosporum* (Sing.) Sing.

*L. heterosporum* (Sing.) Sing. (*Calocybe*, Sing.); *L. venezuelianum* (Dennis) Sing.

Sect 6. *LYOPHYLLUM*. Habit tricholomatoid, more rarely collybioid; spores very variable from globose to fusoid-elongated, from evenly-rounded to subangular, from smooth to verruculose. Context or lamellae, or both characteristically staining yellow, red, blue, or black (or several of these discolorations at the same time, or successively, either upon bruising, or touching, or with age and on drying). Usually on earth or leafmold and solitary or gregarious, rarely cespitose.

*Type species: L. leucophaeatum* (Karst.) Karst.

Subsection *Goniosporina* Sing. (1943). Spores with flattened sides, more or less angular in end-view (polar view), or tetrahedric, rhomboid, sometimes appearing cross-shaped.

*Type species: L. infumatum* (Bres.) Kühner.

*L. infumatum* (Bres.) Kühner; *L. transforme* (Britz.) Sing. (*Tricholoma trigonosporum* (Bres.) Ricken, *Lyophyllum*, Kühner).

Subsection *Globisporina* Sing. (1943). Spores globose to ellipsoid, smooth.

*Type species: L. immundum* (Berk.) Kühner sensu Kühn.

*L. amariusculum* Clém. and several other species (of doubtful standing) in Europe; *L. subnigricans* (Peck) Bigelow in North America, and *L. spadiceum* Sing. ined. (in South America).

Subsection *Buxinea* Sing. (1973). Spores ellipsoid to ovoid, smooth, small; lamellae bux yellow to golden yellow. Staining gray or red before blackening.

*Type species: L. buxeum* (Maire) Kühner & Romagnesi.

*L. favrei* Haller & Haller (and related European species); *L. buxeum* (Maire) Kühner & Romagnesi (North Africa).

Subsection *Semitalina* Sing. (1973). Spores elongated: fusoid or subfusoid-oblong, ellipsoid-cylindric, smooth.

*Type species: L. semitale* (Fr.) Kühner.

*L. semitale* (Fr.) Kühner; *L. capniocephalum* (Bull. ex Fr.) Kühner (sensu Bres.); *L. macrosporum* Sing. (*Clitocybe ectypa* (Fr.) Quél. sensu Bres. non al.).

Subsection *Lyophyllum*. Spores elongated, finely rough to spinulose.

*Type species: L. leucophaeatum* (Karst.) Karst.

*L. fumatofoetens* (Secr.) J. Schäffer (*L. leucophaeatum* (Karst.) Karst.).

Subgenus **Lyophyllopsis** Gerhardt (1982). Clamp connections absent in the hyphae of the carpophore. Spores smooth, ellipsoid or oblong or cylindrical.

*Type species: Lyophyllum incarnatobrunneum* Gerhardt.

*L. incarnatobrunneum* Gerhardt; perhaps also *Rhodocybe marasmoides* Sing.; *Lyophyllum suburens* (Clémenton, and *Clitocybe leucopaxilloides* Bigelow & A.H. Smith.

Note: I have not studied the type species which was however fully described by Gerhardt l.c. whose proposed subgeneric name is here accepted. The other three species indicated above have been considered to belong in *Rhodocybe*. In *R. marasmoides* and *C. leucopaxilloides* the spores are smooth or (some) rounded-angular to subverrucose and these are somewhat rounded-angular in polar view according to my notes on the respective types. Baroni's type studies indicate spores which are round in polar view. In *R. marasmoides* the spore print color is

unknown, but in *C. leucopaxilloides* it is "pale pinkish buff" (Bigelow & Smith). If it were truly pinkish or reddish, these species would key out in the Termitomycteae where, however, they have no affinities. Under these circumstances, the final position of these species is still dependent on the correctness of Baroni's thesis that *Rhodocybe* basidia are not typically siderophilous. The final answer to these problems will probably be the fine structure of the hilum which, according to Pegler & Young (1971) is nodulose in Rhodophyllaceae [Entolomataceae], and of the open-pore type in *Lyophyllum*. On the other hand, *L. suburens* and *L. incarnatobrunneum* have white or "almost white" spore print and are apparently not different from *Lyophyllum* except by clampless hyphae. However, the often irregularly nodulose, elongated spores are in part ± angular in polar view so that this latter character of the spores is obviously not exclusive of *Rhodocybe*.

## 18. CALOCYBE Kühner

*Bull. mens. Soc. Linn. Lyon* 7: 211. 1938 ex Donk, *Nov. Hedwigia* 5: 42. 1962.

*Type species:* *C. georgii* (Clus. ex Fr.) Kühner.

*Syn.:* *Tricholomella* Zerova (cited from *Vizn. Grib. Ukr.* 5(2): 177. 1979).

*Rugosomyces* Raithelhuber, *Metrodiana* 8: 10. 1979.

*Characters:* Those of the family; pileus mostly bright colored, more rarely pale bister or without pigment, but pigment never incrusting or intraparietal, mostly vacuolar; spores usually small, more rarely larger and then frequently echinulate, typically with a hilum of the nodulose type (Pegler & Young); epicutis - a cutis or dense, or cellular; veil sometimes present, more frequently absent. On soil, leafmold, dead wood, in meadows, on lawns, and in the forest.

*Development of the carpophores:* Gymnocarpous in the type species, unknown in other species.

*Area:* Widespread, also in the neotropics.

*Limits:* See under *Lyophyllum*.

*State of knowledge:* 19 species are now known.

*Practical importance:* All species of section 1 are excellent edible fungi often found in European markets.

## SPECIES

Sect. 1. *CALOCYBE*. Pigment not abundant, or absent, if present dull colored or yellow to orangy yellow, never incrusting but mostly vacuolar. Odor usually strong, agreeable, farinaceous. Spores small, smooth. Growing outside the forests, mostly vernal.

*Type species:* *C. georgii* (Clus. ex Fr.) Kühner.

*C. gambosa* (Fr.) Sing. ex Donk; *C. georgii* (Clus. ex Fr.) Kühner; *C. graveolens* (Pers. ex Fr.) Sing.; *C. vasilievae* (Sing.) Sing.\*

Sect. 2. *ECHINOSPORAE* (Lange) Sing. (1943, ut sectio gen. *Lyophylli*). Pileus without or with very little pigment; spores and basidia comparatively large; spores echinulate or rough; cellular epicutis none; stipe with (or without) an annular veil; mostly outside the woods.

*C. constricta* (Fr.) Kühner (Armillaria, Gillet; Tricholoma, Ricken); obviously also *Tricholoma leucocephalum* (Fr. sensu) Lange.

Sect. 3. *PSEUDOFLAMMULAE* Sing. (1943), (*Onychina* Konr. & Maubl. 1948 ut sect. *Tricholomatis*). Pigment of the pileus amber yellow, or wax yellow, perhaps also olivaceous in certain forms, often with more ocher brown or deep blue to violet or red shades; spores smooth; with a cellular epicutis.

Type species: *C. cerina* (Pers. ex Fr.) Kühner sensu Sing. non Kühner.

*C. cyanea* Sing. (Clitocybe, Rick.); *C. cerina* (Pers. ex Fr.) Kühn. sensu Sing. ex Donk (Tricholoma, Kummer); *C. caucasica* Sing.\*\*; *C. onychina* (Fr.) Kühn. ex Donk; *C. fallax* (Sacc.) Sing. ex Redhead & Sing. (*Agaricus fallax* Peck non Lasch; *Tricholoma fallax* (Peck) Sacc.; *Melanoleuca naucoria* Murr., *Calocybe*, Sing.) - Perhaps also *Tricholoma subcerinum* A.H. Smith.

Sect. 4. *CARNEOVIOLACEAE* Sing. (1943). Pigment of the pileus as in sect. 3 above, or pinkish buff to lilac pink, or deep violet to rich blue; spores smooth; epicutis not cellular.

Type species: *C. ionides* (Bull. ex Fr.) Kühner ex Donk.

*C. cyanella* Sing. ex Redhead & Sing.; *C. carnea* (Bull. ex Fr.) Kühner ex Donk (Tricholoma, Kummer); *C. persicolor* (Fr.) Sing. (Tricholoma, Karst.); *C. ionides* (Bull. ex Fr.) Kühner ex Donk (Tricholoma, Kummer Lasch sec. Konrad & Maublanc); *C. fallacissima* Sing. (A. fallax Lasch, Linnaea 4: 524. 1929); *L. alpestris* (Britz.) Huijsman sensu Huijsman; *C. africana* Sing.; *C. coniceps* Sing.; *C. atropapillata* Sing.

## 19. ASTEROPHORA Ditmar ex Fr.

*Syst. mycol.* 1: LI. 1821; 3: 205. 1829.

Type species: *Asterophora lycoperdoides* (Bull. ex Mérat) Ditmar ex. Fr. (= *A. agaricoides* Fr.).

\*c.n. (*Clitocybe vasilievae* Sing., Ann. Mycol. 41: 26. 1943), cf. Harmaja, *Karstenia* 15: 18. 1976.

\*\**Calocybe alpestris* Sing., *Ann. Mycol.* 41: 108. 1943 (see description there, as well as descriptions of *C. naucoria* (Murr.) Sing. and *C. cerina* (Pers. ex Fr.) Sing. - *C. caucasica* Sing. is possibly a subalpine form of *C. naucoria*; it is not *A. alpestris* Britz. which has been rediscovered, with the spore characters more or less as indicated by Britzelmayr.

*Syn.: Nyctalis* Fr., *Stirpes Agri Fem. 3: 58. 1825 \**.

*Asterotrichum* Bon., *Handb. Mykol. p. 82. 1851* (for the chlamydosporic fructification) non  
*Asterotrichion* Klotzsch & Otto (1841).

*Stellifera* Leman, *Dict. Sc. Nat. 33: 489. 1824.*

**Characters:** Those of the tribus; pileus never bright-colored; lamellae often somewhat reduced (rather thick and obtuse, narrow and distant), and production of basidiospores reduced (the more so the more abundant the chlamydospores are); chlamydospores always formed, usually on the mycelium, always on and in the carpophores, in the uppermost layer of the pileus from the surface downwards, or in the lower part of the pileus and in the hymenophore; they are brown, stellate (Pl. 11) or smooth, cyanophilous; habitat: parasitically on Russulaceae. Monomethyl-paramidophenol strongly positive with the context.

**Development of the carpophores:** Gymnocarpous (Reijnders, Corner).

A not regularly observed yeast stage has been described and illustrated by Jahrmann & Prillinger (*Zeitschr. f. Mykologie* 49: 195-226. 1983). It was obtained in certain chlamydospore germinations. This stage, originating, as it seems, from the endospore development inside the chlamydospores, develops later into a pseudomycelium ("pseudotrichial organisation") from which truly "trichial" hyphae and dicaryotic carpophore tissue can be obtained. This is indeed a very important discovery. Although I do not share the far-reaching phylogenetical conclusions suggested by

\* Some authors prefer *Nyctalis* to *Asterophora* but, applying the respective rules, it would appear that Fries's own publications of *Nyctalis* in *Syst. Orb. Veg.* and *Stirpes Agri Femjön. cont. 3* (both 1825) were published independently from *Systema Mycologicum* 1-3 (Jan. 1, 1821 to Dec. 31, 1832) and can therefore not affect the nomenclatorial status of *Asterophora* which was published in the series of *Systema Mycologicum* around 1829, since *Nyctalis* is obviously a synonym of *Asterophora* (*Nyctalis parasitica* being congeneric with *Asterophora lycoperdoides*). Before Donk's interpretation of the starting point rule was accepted by majority vote in Stockholm (1950), the revalidating author of Ditmar's genus would have been Gray. However, Gray's work falls into the same category as Fries's papers of 1825, having been published late in 1821, and since his *Asterophora* is homonymous with Fries's 1829, the legitimate revalidation is in 1829. The solution of the problem depends therefore only on the interpretation of *Asterophora* as an imperfect or as a basidiomycetous genus. If taken as an imperfect genus, i.e. if it is supposed that the chlamydospore-forming tissue of the agaricoid carpophore is a separate state or stage in the life cycle of this organism, *Nyctalis* becomes the valid generic name. This would, however, involve the supposition that Fries has actually meant to separate as an organism or generation apart those hyphae of the carpophore which form chlamydospores; also that it is possible to assume that one part of a carpophore - not life cycle! - can indeed bear a name different from another part of the same individual organ. Since such an assumption is neither in agreement with the letter of the Code nor within the intellectual capacity of the present author, the name *Asterophora* is here preferred. Donk (*Taxon* 13: 16. 1964) argues that "even if the type material had developed basidia (but this is not quite certain), the description [by Fries] directs the application of the name in such a manner that *Asterophora* [is] to be treated as a [nomen] anamorphosium". What he means to say is that Fries gave emphasis to the presence of "sporidia" and did not actually observe (he almost never did!) the basidiospores, thus thinking the fungus is a Gasteromycete and, by the way, not a "Coniomycete" or Hyphomycete! Why this should make *Asterophora* a state in a pleiomorphic life cycle is not clear and can only be understood in the light of Donk's very personal interpretation of the rules ("Fries ... was convinced that the 'species' was non-agaric"). In the opinion of most mycologists, in this context, it is not important what Fries was convinced of having, but what he must have had. In this case we know perfectly well what Fries had because he describes the "adnate, distant, thick lamellae" which he considered normal and which always develop basidia; he even suspected that the second species (l.c. p. 206) with smooth lower surface is a young sterile state of *A. agaricoides*. Consequently, the type of *Asterophora* is an agaric.

these authors, as long as only one species in one order has been studied, it certainly calls to mind the "mycotètes" with the blastospores described by Heim and others in *Termitomyces*. See also p. 8 and 228.

**Area:** Not fully established; found in Europe, North America, south to Cuba and also in East Asia, south to the mountains of New Guinea.

**Limits:** The habitat and the manner of reproduction distinguish this genus sufficiently.

**State of knowledge:** Many dubious species were described in *Nyctalis* but it is probable that the genus *Asterophora* contains only two species. These are completely known.

**Practical importance:** None. Eichelbaum described a *Nyctalis coffearum* causing "splitting disease" of *Coffea* but this species is not an *Asterophora* but, according to Roger (1951), *Armillariella fuscipes* (Petch) Sing.

## SPECIES

*A. lycoperdoides* (Bull. ex Mérat) Ditmar ex Fr. (*Nyctalis asterophora* Fr.; *Asterophora agaricoides* Fr. ex Fr.; *Nyctalis nauseosa* Weinm.); *A. parasitica* (Bull. ex Fr.) Sing. (*Nyctalis*, Fr.).

## 20. HYPISIZYGUS Sing.

*Mycologia* 39: 77. 1947.

**Type species:** *H. tessulatus* (Bull. ex Fr.) Sing. (sensu Singer = *Pleurotus ulmarius* auct. Amer.)

**Characters:** Pigment little, sometimes grayish or ochraceous in parts of the carpophores when adult, and this pigment neither vacuolar nor strongly incrusting; carpophores nearly tricholomatoid, but rarely more clitocyboid, and often with a ± eccentric stipe, non-luminescent, thick-fleshy, dried hard and not fragile, non-hygrophanous, not viscid, often in age areolate-rimose; lamellae adnexed to adnate and emarginate or sinuate or else decurrent or at least with lines short-decurrent on the white apex of the stipe continuing the lamellae which easily separate from the flesh or at least the apex of the stipe. Spore print pale cream or light ochraceous or pure white when quite fresh. Spores small (3.5-7  $\mu\text{m}$ ) broad-ellipsoid to ovoid or subglobose to globose, hyaline, the wall becoming firm, carminophilous, cyanophilous, inamyloid, smooth. Basidia generally 4-spored, clavate, without siderophilous granulation but mostly some mature basidia with siderophilous granulation of the *Oligo*-type mixed in; cystidia absent. Hymenophoral trama strictly regular of parallel or subparallel filamentous hyphae, few somewhat inflated, hyaline, non-gelatinized. Hyphae of the pileus trama thin- to moderately thick-walled (wall to 0.8  $\mu\text{m}$ , inamyloid); hyphal system monomitic. Subhymenium very

narrow, ramosc. Clamp connections numerous. Veil none. Always lignicolous, on trunks of trees (frondose trees: *Ulmus*, *Acer*, etc.) often high up on living trees, parasitic or saprophytic.

*Development of the carpophores:* Unknown.

*Area:* Mainly in temperate North America, Europe, Asia; circumpolar.

*Limits:* Traditionally, this is a *Pleurotus* but differs from all Polyporaceae in the spores. American mycologists have determined the type species as *Pleurotus ulmarius* in the past. The European *P. ulmarius* however, is not conspecific.

*Hypsizygus* is perhaps the genus most closely related to the Tricholomataceae because of the weak siderophily of the basidia but close to *Lyophyllum* because of the cyanophilous, carminophilous spores. It differs from *Lyophyllum* not only in the scantier siderophilous granulation in the basidia but also in the absence of conspicuous incrusting and intraparietal pigment, its lignicolous habitat and also frequently parasitic condition, and its hard, non-fragile context when dried. It differs from *Calocybe* by its habitat, habit, and scantier siderophilous granulation in the basidia.

*Hypsizygus* is comparable to *Clitocybe* sect. *Lignatiles* which differs in consistency and habit, in acyanophilous, non-carminophilous spores, and smaller basidia.

*State of knowledge:* Five species are completely known.

*Practical importance:* It is certain that *Hypsizygus tessulatus* causes wood rot on previously undiseased elms and contributes to the death of older trees. The carpophores are eaten by American Indians as well as by a small part of the white population in North America, and by some mushroom hunters in East Asia. *H. ulmarius* is also edible and is parasitic on frondose trees. *H. tessulatus* is parasitic mainly on *Acer negundo* and some species of *Ulmus*.

## SPECIES

*H. tessulatus* (Bull. ex Fr.) Sing. sensu Sing.\* (Pleurotus Gillet; Pleurocybella, Moser apud Gams; Pleurotus "ulmarius" auct. Amer. non sensu Kühner); *H. ulmarius* (Bull. ex Fr.) Redhead (Agaricus ulmarius Bull. ex Fr., Syst. Myc. 1: 186. 1821); *H. circinatus* (Fr.) Sing.; *H. marmoreus* (Peck) Bigelow (?*Lyophyllum shimedyi* (Kawamura) Hongo); *H. elongatipes* (Peck) Bigelow.

## Tribus *Termitomycteae* (Jülich) Sing. st. nov.

*Type genus:* *Termitomyces* Heim.

*Syn.:* Family *Termitomyctaceae* Jülich, *High. Taxa Basid.* p. 391. 1981 (basionym).

\*Fully described in Singer & Kuthan, *Česká Mykologie* 34: 57-60. 1980. The interpretation of Bulliard's plate is not yet definitively proven.

**Characters:** Those of the family; basidia (where studied) of the *Lyophyllum*-type i.e. with siderophilous granulation in the mature stage; spore print light pink to Etruscan red; spores smooth, rarely subsMOOTH, inamyloid, cyanophilous; hyphae inamyloid, without clamp connections; hymenophoral trama either regular or bilateral; often termitophilous (but what might be called a symbiotic relationship with the termites only in *Termitomyces*); otherwise on dead plant material, on earth, or humus.

**Note:** The data on which the insertion of this tribus near the Lyophylleae and its reognition are based, viz. the siderophilous basidia and cyanophilous spores were first observed respectively confirmed in *Podabrella* by Cléménçon (in litt.) and further investigated in *Termitomyces* by him. Presently, enough species of *Podabrella* and *Termitomyces* are known to have siderophilous granulation and cyanophilous spores to tentatively consider these characteristics to be general in this tribus. Studies under the SEM might reveal that the open-pore hilum, characteristic for *Lyophyllum* spores and indicated also for *Termitomyces* (Pegler & Young 1971), is likewise general for the Termitomyceteae. The clampless species of *Lyophyllum* may well be interpreted as transitional between the two tribus but since the shape of the carpophores differs from that of the Termitomyceteae and all are north-temperate or subtropical rather than tropical, they are closer to *Lyophyllum* than to the Termitomyceteae. Nevertheless, the Lyophylleae and Termitomyceteae are closely enough related to be separated from the rest of the tribus under a subfamilial name. This, at present, does not appear to provide any advantage and would merely complicate the suprageneric taxonomy of the Tricholomataceae even further.

#### KEY TO THE GENERA

- A. Carpophores relatively small, mycenoid to collybioid, without a true pseudorrhiza and without a distinct veil in mature specimens, with adnate to subfree lamellae, growing superficially on termite nest material or on dead plant remains or humus or earth. 21. *Podabrella* p. 226
- A. Carpophores more fleshy, pluteoid, with a long pseudorrhiza tapering downwards and often with a persistent veil, with free lamellae, rising from the hypogeous "mycotôtes" with primordia inside the termite nests. 22. *Termitomyces*, p. 228

#### 21. PODABRELLA Sing.

*Lloydia* 8: 143. 1945.

**Type species:** *Collybia microcarpa* (Berk. & Br.) Hoehnel sensu Hoehnel.

**Syn.:** *Termitomyces* subgen. *Praetermitomyces* Heim, *Arch. Mus. Nat. Hist. Nat.* VI ser. 18: 147. 1941.

**Characters:** Those of the tribus. Habit of the carpophores mycenoid-collybioid; pileus with an epicutis consisting of thin, repent, parallel, hyaline, smooth, filiform hyphae; sometimes with occasional nests of intricately interwoven hyphae or with narrow dermatocystidia; hypodermium consisting of somewhat broader hyphae which are contracted at the septa, likewise hyaline (the whole fungus often with little or no pigment) and elongate; lamellae subfree to adnate, thin, intermixed with

lamellulae; spore print pale rose color to "Etruscan red" (M. & P.); spores hyaline under the microscope, rather thin-walled, inamyloid, ellipsoid to ovoid or subcylindric, sometimes indistinctly rough or uneven but wall generally smooth and homogeneous; basidia rather small, normal for the tribus; cystidia usually none or few, but cheilocystidia present, these often making the edge of the lamellae heteromorphous or else turning them discolored by a necropigment; trama of the hymenophore regular; stipe solid, rather thin, without distinct pseudorrhiza or with a hypogeous pseudorrhiza-like prolongation, the context of the type species rather soft, the latter rising from small globulose white bodies which are ejected from termite nests by the termites ("mycotêtes", according to Heim); context fleshy, unchanging, consisting of hyphae which are devoid of clamp connections inamyloid. On earth, rotting plant débris, also on termite nests.

*Development of the carpophores:* *P. microcarpa* is most probably hemiangiocarpous, certainly not gymnocarpous according to Heim whose observations are interpreted by Reijnders as showing bivelangiocarpous development.

*Area:* Tropical and subtropical in both hemispheres.

*Limits:* The genus is clearly different from *Termitomyces*. Even in the type species the "symbiosis" with termites is much less intimate while in the neotropical species no termitophily can be observed. Furthermore, there are differences in size and habit of the carpophores, and a true pseudorrhiza is not developed; a veil is constantly absent in mature specimens.

A few species agree well with *Podabrella* but their exact spore print color has not been determined. One is a species determined *Collybia alba* by A.H. Smith, collected by me in Florida, another is a new species, *Podabrella albida* Sing. ined. from Costa Rica. Neither of these is termitophilous. Whenever data about the spore print color become available, the position of these species may be solved definitely.

*State of knowledge:* Four species are known.

*Practical importance:* It had been believed that *P. microcarpa* plays an important rôle in the nutrition of the termites in the palaeotropics, and thus might have some indirect practical importance, when Heim restudied this relationship. He came to the conclusion that the termites are compelled to rid their nests of this "Haus-schwamm", and use it only occasionally for food; the larvae are not fed fungi at all. The practical importance of these fungi consists therefore exclusively in their value for human consumption. *P. microcarpa* is thought to be one of the most delicious edible fungi of the regions where it is common, and is by some considered to be superior to all other species.

## SPECIES

*P. microcarpa* (Berk. & Br.) Sing.; *P. epipolia* Sing.; *P. poliomphax* Sing.; *P. albida* Sing. (the last three neotropical, ined.)

## 22. TERMITOMYCES Heim.

*Arch. Mus. Nat. Hist. Nat. ser. 6, 18: 147. 1942.*

*Type species:* *T. striatus* (Beeli) Heim.

*Syn.:* *Rajapa* Sing., *Lloydia* 8: 142. 1945.

**Characters:** Habit of the carpophores pluteoid, usually rather fleshy and large, with prominent, often very sharply differentiated umbo; stipe central; spore print pink; lamellae free to ± adnexed but then emarginate or with decurrent tooth; stipe with a pseudorrhiza and with a simple or double veil, or evelate. Epicutis (excepting the region on and near the umbo in certain species) consisting of repent filamentous, hyaline hyphae; hymenophoral trama bilateral in the primordium, often remaining so for a relatively long time, but in adult specimens mostly quite regular and consisting of parallel, thin-filamentous hyphae; spores hyaline, inamyloid, with a hilum of the open-pore type (according to Pegler & Young 1971), ellipsoid, smooth, with homogenous wall; basidia normal for the tribus; cystidia mostly present; tramal hyphae inamyloid, without clamp connections, not gelatinized. Tramal system strictly monomitic. The primordia develop in the holes of termite nests.

*Development of the carpophores:* "Hemiangiocarpous" according to Heim, interpreted as bivelangiocarpous by Reijnders, at least in the type species.

**Area:** Tropics of Asia, Africa, and the South Pacific.

**Limits:** Heim considers *Podabrella* a subgenus of *Termitomyces*. The two genera are undoubtedly closely related. However, in *Podabrella* (sg. *Praetermitomyces* Heim) the primordia do not develop within the termite nests, and the carpophores are devoid of constant and true pseudorrhiza (attached to a widened and/or subbulbous stipe-base, gradually tapering and not rounded at the bottom) and veil; the epicutis of the pileus is always and in all parts a cutis rather than a trichodermial palisade or a hymeniform structure. Horak (1968) on the other hand, wishes to leave the possibility open that *Rajapa*, based on *Agaricus eurhizus* Berk. is not congeneric with *Termitomyces*. Young specimens of *T. eurhizus* seemed to me to maintain a bilateral or subbilateral structure longer than other species of the genus, e.gr. *T. cartilagineus*, but *T. congolensis* showed a more distinct bilateral trend as well as *T. letestui*, whereas different material of *T. eurhizus* gave different results. There is apparently as much variability as there is in other Tricholomataceae with slightly bilateral trama (e.gr. *Flammulina*) and since the character appears to be somewhat variable as soon as the primordial stage is passed, I do not think that the genus *Termitomyces* can be divided into two according to bilaterality. On the other hand, the type of bilaterality often encountered in *Termitomyces* is of an entirely different kind as compared with that of *Amanita* and is also not comparable with that of *Limacella*; thus, there is no reason why the genus should be maintained in the Amanitaceae.

**State of knowledge:** It is the merit of Heim that we know the genus well, particularly in tropical Africa\*. He has studied several species from many points of view, and his

\*see Heim (1952) and *Flore iconographique des champignons du Congo*, *Termitomyces*, with further bibliographic notes.

work on the genus is classical as well as thorough. The types of some Asiatic and two African species have been restudied by the present author, who found well-preserved alcohol material at Berlin-Dahlem. 13 species are enumerated below.

**Practical importance:** Most species are highly valued edible mushrooms gathered by the bushel each season in Africa as well as in Asia. They are indirectly linked with the economical importance of the termites because of their rôle in the biology of many termite species.

## SPECIES

### 1. African species:

*T. citriophyllus* Heim; *T. fuliginosus* Heim (perhaps a variety of the following); *T. robustus* (Beeli) Heim; *T. striatus* (Beeli) Heim (perhaps a variety of *T. cartilagineus*); *T. mammiformis* Heim; *T. letestui* (Pat.) Heim; *T. schimperi* (Pat.) Heim; *T. congolensis* (Beeli) Sing. (perhaps a variety of *T. letestui* or *T. schimperi*); obviously also *T. globulus* Heim & Gooss. and *T. clypeatus* Heim; apparently also *T. eurhizus* (see under 2 below).

### 2. Asiatic species (possibly all identical with each other):

*T. eurhizus* (Berk.) Heim; *T. cartilagineus* (Berk.) Heim; and the following species (types seen): *Flammula janseana* Henn. & Nym.; *Flammula filipendula* Henn. & Nym., obviously also *Agaricus (Pluteus) rajap* Holtermann.

## Tribus *Tricholomataceae* (autonym)

**Type genus:** *Tricholoma* (Fr.) "Staude".

Syn.: *Tricholomataceae* Fayod (ut *Tricholomés*), l.c., p. 346; *Lotsy, Vortr. Bot. Stamm.-gesch.* 1: 713. 1907 (*Tricholomeae*); Imai, *Journ. Fac. Agr. Hokk. Imp. Univ.* 43: 64. 1938.  
*Clitocybeae* Fayod ex *Lotsy, Vorträge Bot. Stamm.-gesch.* 1: 711. 1907.

**Characters:** Those of the family; basidia not of the *Lyophyllum*-type, without siderophilous granulation; spores inamyloid; hyphae inamyloid; hymenophore lamellate, venose, or absent; hymenophoral trama regular to somewhat irregular, sometimes with a *Clitocybe*-subtype structure, but not bilateral (excepting the primordia); true cystidia rarely present (excepting some species of *Clitocybe*, *Tricholomopsis*, and *Cypholostereum*), but pseudocystidia often present and at times conspicuous (like the gloeocystidia of *Lactocollybia* and *Macrocystidia*); habit of the carpophores mostly clitocyboid, tricholomatoid or omphalioid, more rarely pluteoid or pleurotoid, but in the latter case a distinct, well developed stipe present, excepting some cyphelloid (reduced) forms; epicutis consisting of a little differentiated (dense) layer or represented by a cutis, more rarely a rather undifferentiated trichodermium, but not cellular (excepting one section of *Clitocybe*), not showing a *Rameales*-structure nor acanthocyst-like elements, but sometimes with more or less scattered dermatocystidia or dermatopseudocystidia; white or black rhizomorphs

scattered dermatocystidia or dermatopseudocystidia; white or black rhizomorphs often present (black rhizomorphs only in species without clamp connections in the trama); trama not reviving after exsiccation, nor showing gelatinous layers; hyphae with or without clamp connections. On the earth or humus, on vegetable rests, on termite nests, rarely parasitic, mostly saprophytic, sometimes ectomycorrhizal or endomycorrhizal, but only in some subgenera of *Tricholoma* obligatorily ectomycorrhizal, sometimes growing on living mosses.

#### KEY TO THE GENERA (AND SUBTRIBUS)

- A. Clamp connections constantly present; spore print white, pale cream, pale livid to amethyst, dirty pinkish to salmon pink, rarely pale greenish or yellow; hymenophore always present in form of veins or lamellae.
  - B. Hymenophore in form of veins (see "C" key II below).
  - B. Hymenophore in form of well developed lamellae.
    - C. Gloeocystidia numerous and/or a latex and laticiferous hyphae present carpophores (see "EE" Key II below).
    - C. Gloeocystidia none and latex and laticiferous hyphae absent.
      - D. Spores globose to cylindrical (and then very large), varying from finely asperulate at least under SEM) to strongly echinate-spinulose, in print varying from pure white to light amethyst; development of the carpophores hypovelangiocarpous, at least in the type species (*L. laccata*); lamellae somewhat thickish, pale ochre isabelline to pinkish-flesh color or lilac; hymenophoral trama quite regular, consisting of ± parallel hyphae; cheilocystidia and cystidioles mostly present but very inconspicuous; spores including the ornate acyanophilous to weakly cyanophilous all over (not showing strongly cyanophilous ornamentation on acyanophilous ground). Growing on the ground, more rarely on sand, volcanic ashes, often among mosses, charcoal, on Sphagnum, dunes, and rarely on rotten wood; ectotropically mycorrhizal but only facultatively so but capable to assimilate polysaccharids; pigments sometimes (but typically not) incrusting the cell walls.  
*Laccariinae*:  
23. *Laccaria*, p. 233
      - D. Spores smooth or finely to coarsely verruculose (but then the ornamentation distinctly cyanophilic on non-cyanophilic ground and lamellae thin; gymnocarpous); not combining all the characters indicated above.  
*Clitocybinae*
      - E. Spores angular in polar view or verruculose or both, often pinkish in print.
        - F. Spores angular in polar view and evenly cyanophilic (see Entolomataceae).
        - F. Spores not at the same time angular in polar view and evenly cyanophilic (if the spores are subsMOOTH in light microscopy, they are rough in SEM view and then the spore print is not white).  
25. *Lepista*, p. 247
      - E. Spores neither angular in polar view nor verruculose, but terete or evenly ellipsoid to globose and smooth, evenly cyanophilic or acyanophilic, sometimes cross-shaped or subangular but then spore print white or whitish and habit tricholomatoid.
        - G. Spores at the same time strongly cyanophilic and carminophilic, mostly short ellipsoid to globose, small. Lignicolous species, tricholomatoid-pleurotoid or clitocyboid-pleurotoid (see Lyophylleae).
        - G. Spores either acyanophilic or weakly cyanophilic, spores habitat and habit as above or different.
          - H. Cheilocystidia large and conspicuous; (pleuro-) cystidia also at time present; edge of lamellae heteromorphous or subheteromorphous; pileus fleshy, fibrillose or squamulose or even squarrose, neither hygrophanous nor viscid, often bright colored; stipe central, more rarely slightly eccentric, well developed, growing on dead wood or connected with buried wood by conspicuous white rhizomorphs; habit tricholomatoid.  
26. *Tricholomopsis*, p. 251

H. Cheilocystidia not large and conspicuous, or else not combining the characters indicated above.

I. Habit tricholomatoid.

- J. Pileus green or spores pink or greenish in print; spores neither cross-shaped or subangular; odor often anise-like; pileus not viscid (see "L")
- J. Pileus not green; spores not pinkish or greenish; spores subglobose to ellipsoid or cylindric; odor not anise-like; epicutis sometimes an ixocutis (see "DD").

I. Habit clitocyboid or omphaloid, rarely more collybioid or pleurotoid.

- K. Strictly omphaloid, always pigmented with a intraparietal and at least in parts of the carpophores strongly incrusting, dark, rarely bright colored (green, purplish) pigment; pileus not hygrophanous; on sandy soil, earth, Sphagnum and other mosses, algae, dead wood, often boreal or alpine (not tropical), often lichenized. (see "BBB" key III).

K. Not combining the characters indicated above.

- L. Omphaloid without intraparietal or incrusting pigment and with rather cartilaginous stipe; pigment either pink or xanthic or carotenoids present, or else mainly tropical species. (see "BBB" key III).

- L. Clitocyboid or subomphaloid and then either without any pigment or with intraparietal or incrusting pigment. Temperate as well as tropical, boreal or alpine species.

24. *Clitocybe* p. 236

A. Clamp connections absent in the carpophore (see key II).

#### KEY II (SUBTRIBUS OMPHALINAE)

AA. Hymenophore often or always reduced to veins or hymenium on a smooth surface; habit spatuloid, pleurotoid, cyphelloid; often muscicolous. (Reduced series of *Omphalinæ*)

BB. Hymenophore venose (veins sometimes anastomosing); pigments not absent but generally incrusting, intraparietal, gray, fuscous or blackish bister; clamp connections present or absent; cystidia none.

CC. Young carpophore cupuliform, later spoon shaped, nutant.

Reduced series: 31. *Arrhenia* p. 265

CC. Carpophore differently shaped. Mostly muscicolous.

Reduced series: 32. *Leptoglossum* p. 266

BB. Hymenophore mostly none, hymenal surface smooth or somewhat canaliculate on some carpophores; pigment none; clamp connections none.

CC<sub>1</sub> Hyphae not inflated.

Reduced series: 41. *Cyphellostereum* p. 286

CC<sub>1</sub> Hyphae inflated to 22µm; cystidia absent (see *Semiomphalina*, p. 853)

AA. Hymenophore always well developed, lamellate.

DD. Habit strictly and constantly tricholomatoid; spores without pigment bodies (appearing as necropigment); spore print white to palest cream, not pink; black rhizomorphs not formed in mycelial cultures; mycelium not luminescent, not parasitic but often (not always) ectotrophically mycorrhizal (not endotrophically mycorrhizal); generally neither muscicolous (but may grow among mosses) nor lignicolous; spores sometimes cruciform or subangular (and then not ectotrophically mycorrhizal), but more frequently not so

*Tricholomatinae*, see key III.

DD. Habit not tricholomatoid (or not distinctly or constantly so). Not combining the characters indicated above.

EE. Gloeo-vessels and gloecystidia and/or laticiferous hyphae present, numerous or conspicuous, or latex present in the lamellae.

FF. Spores star-shaped, strongly nodose or nodulose.

GG. Hyphae without clamp connections; pigments fuscous to gray. Temperate, often boreal or alpine species (see *Hygrophoraceæ*).

GG. Hyphae with (often scattered and in part atypical) clamp connections; pigments generally more vividly colored. Tropical species.

40. *Asproinocybe*, p. 285

FF. Spores smooth under the light microscope (may be rugulose, SEM).

HH. Spore wall thin, quite hyaline, not bistratous; spore print white.

37. *Lactocollybia*, p. 281

HH. Spores double walled, somewhat stramineous or palest pinkish stramineous in KOH; spores mostly not pure white in print.

II. Hyphae of the carpophore with clamp connections; pileus not pectinate; stipe without a margined bulb. 38. *Macrocystidium*, p. 283

II. Hyphae without clamp connections; pileus pectinate; stipe with a margined bulb. 39. *Fissolimbus*, p. 284

EE. Gloeo-vessels and gloecystidia none; laticiferous vessels, none; latex, none.

JJ. Intracellular necropigments conspicuous in spores and often also in hymenial elements; hyphae always without clamp connections; habit collybioid, mycenoid, rarely almost tricholomatoid. 35. *Callistosporium*, p. 278

JJ. Spores without necropigments, spore interior in dried specimens hyaline.

KK. Mycelium, at least in cultures, forming black rhizomorphs; stipe often annulate; habit ± clitocyboid; spore print white or cream when fresh; hyphae without clamp connections (but clamps often present at base of hymenial cells, sometimes even at base of external cells of epicutis); development including a diploid phase. Lignicolous, often parasitic or forming endotrophic mycorrhiza, more rarely sphagnicolous; sclerified basidia often observed.

28. *Armillariella*, p. 261

KK. Mycelium not forming black rhizomorphs; annulus absent; clamp connections present or absent; development (as far as known) not including a diploid phase; habitat as above, or different; sclerified basidia generally not formed.

LL. Clavarioid arthrospore-bearing carpophores preceding the basidiospore-bearing clitocyboid carpophores; clamp connections absent.

29. *Arthrosoparella*, p. 264

LL. Only basidiospore-bearing carpophores known (see key III).

### KEY III (OMPHALINAE, PART; TRICHOLOMATINAE)

AAA. Habit omphaloid.

BBB. Pigment intraparietal and often incrusting; spore print white, more rarely pink; clamp connections present or absent. 33. *Omphalina*, p. 269

BBB. Pigment intracellular (rarely intercellular and incrusting around special hyphal systems), or completely absent (if completely absent, usually without clamp connections); spore print white, cream, or yellow to orange salmon. 34. *Gerronema*, p. 272

AAA. Habit not omphaloid.

CCC. Habit clitocyboid.

DDD. Epicutis dense, or a cutis (see key I, "L").

DDD. Epicutis - a trichodermium

30. *Lulesia*, p. 264

CCC. Habit tricholomatoid, collybioid, or pleurotoid.

EEE. Epicutis - a trichodermium (see "DDD" above).

EEE. Epicutis dense, or a cutis.

FFF. Habit tricholomatoid; not lignicolous

27. *Tricholoma*, p. 253

FFF. Habit collybioid to pleurotoid; often lignicolous.

GGG. Carpophores entirely white or entirely yellow (cf. *Gerronema*, *Collybia*).

GGG. Carpophores not entirely white nor entirely yellow; spores small, often pleurotoid 36. *Pleurocollybia*, p. 279

Subtribus *Laccariinae* (Jülich) Sing. (stat. n., Lacciaceae Jülich, High. Taxa Basid. p. 374. 1981, basionym). Spores echinate-spinulose or at least asperulate (in light microscopy often appearing subsMOOTH but then long and cylindric), the ornamentation not entirely strongly cyanophilic on acyanophilic ground; clamp connections present; spore print white or amethyst; (all or many) facultatively ectomycorrhizal.

Type genus: *Laccaria* Berk. & Br.

## 23. LACCARIA Berk. & Br.

*Ann. Mag. Nat. Hist.* 5: 370. 1883.

Type species: *Laccaria laccata* (Scop. ex Fr.) Berk. & Br.

Syn.: *Russuliopsis* Schröter in Cohn, *Krypt. F. Schles., Pilze*, p. 622. 1889.

**Characters:** Pileus dry to subhygrophanous, glabrous to squamulose, smooth to transparently striate when moist; cuticle not strongly differentiated; lamellae rather thick and somewhat distant, moderately broad to extremely broad, usually bright colored (blue, lilac, violet, pinkish vinaceous, rose color, yellow); hymenophoral trama strictly regular to almost regular; spores (Pl. 46, 1-3) either oblong and voluminous (11-22  $\mu\text{m}$  long), or short-ellipsoid to globose and then echinate, the spines conical but sometimes curved and arranged in spirals inamyloid superimposed on and heterogeneous in relation to an episporium which is continuous and likewise inamyloid\*; spore print white or "pale Verbena violet"; basidia frequently two-spored, otherwise four-spored, without carminophilous granulation, cystidia none, but cystidioles sometimes and cheilocystidia mostly present although often scattered and inconspicuous; trama fibrous-fleshy, not reviving, inamyloid; pigments not conspicuous microscopically, not incrusting the hyphal walls, all hyphae with clamp connections. On soil, among deep moss, in clearings, in deep woods, in alpine pastures, along brook beds, on decayed wood, on leafmold, on charcoal, on sandy and volcanic soil, and on rocky places. Ferric sulphate causing a distinct deep gray discoloration in the species tested.

**Development of the carpophores:** *Laccaria laccata* (see Reijnders 1943, pl. V, fig. 7) hypovangeliocarpous since the "angiocarpous" phase is of short duration, and the covering even then very thin (Reijnders 1948), monovelangiocarpous, stipitocarpous acc. to Watling (1985).

**Area:** Cosmopolitan. Even some of the infraspecific taxa have remarkably large areas of distribution.

**Limits:** *Laccaria* is easily distinguishable from the other clamp-bearing Clitocybeae on the basis of spore characters, the structure of the hymenophoral trama and the colors of the lamellae and their thickness, the absence of a veil and the characteristic (not fully clitocyboid) habit, the chemical and embryological characteristics, and the

\*For more detailed observations (EM) see Besson (1976), Kühner (1980) p. 338 [518] fig. 141-142 (taken from Besson).

color of the spore print - although none of these characters alone is fully constant or exclusive in the genus.

As for the position of *Cantharocybe* which in spite of the smooth spores (light microscopy) is anatomically similar to *Laccaria*, at least *L. trullisata*, see p. 111.

The not fully gymnocarpous development, the frequent occurrence of aborted or monstrose carpophores, the spores as seen in *L. echinosperma*, the striking similarity of the colors, and the facultative or pseudoectomycorrhizal relationships as well as the presence of clamp connections suggest that *Laccaria* may indeed present rather close phylogenetic relationships with *Hydnangium*-like fungi as well as with Clitocybinae. These relationships have been recognized by Romagnesi (1967), myself in Singer & Smith (1960) and singer (1975), Pegler & Young (1979), Kühner (1980), and Beaton, Pegler & Young (1984). Kühner (1980) went one step further by inserting *Laccaria* in the Hydnangiaceae. It is however often overlooked that *Hydnangium* and even *Podohydnangium* are true Gasteromycetes with apobasidia and not producing a spore print, growing hypogeaously or subhypogeaously, sporulating within the gleba and the peridium, lacking an epigeous stipe and ordinarily a percurrent columella; besides, at least in two species, numerous laticiferous hyphae are present in *Hydnangium* (as they are often in Elasmomycetaceae) but not in *Laccaria*, and lactocystidia as well as spherocysts are found in *Hydnangium soederstroemii* in the trama of the peridium. These characteristics approach them to the "asterosporaceous series" i.e. Elasmomycetaceae, a fact recognized by Malençon (1931), Singer & Smith (1960), Beaton, Pegler & Young (1984) and others. It follows that the inclusion of *Laccaria* in the Hydnangiaceae makes sense only if (1) Russulaceae and Elasmomycetaceae are joined with Hydnangiaceae and *Laccaria* into a single family and (2) Gasteromycetes as an order or super-order are abandoned. See also p. 252.

*State of knowledge:* 18 species have now been clearly defined.

*Practical importance:* All species enumerated below are edible. As facultative ectomycorrhizal fungi, the Laccarias - or many of them - have an important rôle in forest succession (see Singer in Haczkaylo, 1971). This is an important factor in forestry inasmuch as mycorrhizal synthesis both in the laboratory and in nurseries is relatively easily established with the Laccarias which grow more rapidly in agar and submerged culture than most obligatory ectomycorrhizae.

## SPECIES

Stirps *Trullisata* (with smooth to asperulate, strictly elongated, large spores): *L. trullisata* (Ellis) Peck; *L. maritima* (Theodorowicz) Sing. (the latter apparently only a geographic race of *L. trullisata*).

Stirps *Amethystina* (with echinate spores; spore print white or light amethyst; lamellae violet to dull livid-pink): *L. ochropurpurea* (Berk.) Peck; *L. bicolor*

(Maire) Orton; *L. calospora* Sing. (L. amethystina aut. p.p.\*); *L. amethystina* (Bolt. ex Hooker) Murr. (L. amethystinooccidentalis Müller); probably also *L. lilacina* Stevenson.

Stirps *Laccata* (with echinate spores; spore print white; lamellae flesh-pink): *L. laccata* (Scop. ex Fr.) Berk. & Br. (with several forms and varieties); *L. farinacea* (Huds. ex S.F. Gray) Sing.\*\*; *L. proximella* Sing.; *L. proxima* (Boud.) Orton sensu Favre, Sing.; *L. tetraspora* Sing.; *L. montana* Sing.; *L. altaica* Sing.; *L. echinospora* (Speg.) Sing.\*\*\*; undoubtedly also in this stirps: *Agaricus ohiensis* Mont.\*\*\*\*

Stirps *Galerinoides* (with echinate, short spores, pale ochraceous-isabelline or livid-avellaneous): *L. galerinoides* Sing. in Sing. & Moser; *L. vinaceoavellanea* Hongo.

Stirps *Purpureobadia* (like stirps *Amethystina* or *Galerinoides* but with incrusting pigment): *L. purpureobadia* Reid; possibly *Rhodocybe nauseodulcis* Horak (Omphaliaster, Noordeloos).

Subtribus *Clitocybinae* Sing. subtrib. nov.\*\*\*\*\*

*Characters:* Spore not as in *Laccaria*, smooth or with cyanophilous ornamentation; clamp connections generally present; habit clitocyboid, or, if tricholomatoid, spores ornamented or cheilocystidia prominent; gloeocystidia none.

*Type genus:* *Clitocybe* Kummer.

\*e.gr. Aguirre Acosta & Pérez Silva

\*\*Since Bolton, *Hist. Fung.* 1: 64 (plate) and Persoon's (1801 and 1822) descriptions agree sufficiently with Persoon's material (L) studied by me and Gray's understanding of this binomial must have been based on the older British literature I believe that my interpretation of *L. farinacea* is correct and L 910.258-582 is herewith proposed as neotype. Dr. Müller (personal communication) informed me that species identified as *L. farinacea* sensu Sing. and *L. bicolor* respectively were interfertile in mating experiments. If this is confirmed, *L. bicolor* would become a form of *L. farinacea* (see also Fries & Müller, *Mycologia* 76: 633-642. 1984).

\*\*\*This species is often called *L. tortilis* (Bolt. ex Fr.) Pat., but Bolton's fungus as well as that of Fries may well be a small form of *L. tetraspora* or *L. fraterna*.

\*\*\*\*The type was studied by Singer and both 2- and 4-spored carpophores were found. The 2-spored carpophores were taken as lectotype but were lost at FH; the rest was restituted to P where according to newer type studies (Malençon, Bon, Müller) only 4-spored forms remain. Under the circumstances, I see no alternative but to abandon the binomial *Laccaria ohiensis*. However, the correct name for the 2-spored species similar to *L. tetraspora*, if not *L. ohiensis*, must be *L. fraterna* (Cooke & Mass.) c.n. (*Agaricus fraternus* Cooke & Mass., *Grevillea* 16: 31. 1887), not *L. lateritia* Mal.

\*\*\*\*\*Sporis levibus vel verruculis cyanophilis obsitis; hyphis fibulatis; carpophoris citocyboideis vel tricholomatoideis sed tunc sporis verruculosis aut cheilocystidiis prominentibus, gloeocystidiis hyphisque laticiferis nullis.

## 24. CLITOCYBE Kummer

Führ. Pilz., p. 26. 1871.

Type species: *Clitocybe gibba* (Pers. ex Fr.) Kummer \*.

Syn.: *Agaricus tribus Clitocybe* Fr., Syst. Mycol. 1: 78. 1821, p.p.

*Clitocybe* (Fr.) Quél., Champ. Jura Vosges, p. 85. 1872-73.

*Omphalia* Quél. Enchir., p. 19, 1886, non (Pers. ex) S.F. Gray (1821), nec (Fr.) Quél. (1872-73);  
nec *Omphalea* L. 1756 nom. conserv.

*Trigonipes* Velen., Novit. myc., p. 77. 1939.

*Singerella* Harmaja, Karstenia 14: 113. 1974, non *Singeriella* Petrak, Sydowia 12: 252. 1958.

**Characters:** Carpophores of strictly clitocyboid habit, rarely pleurotoid, often depressed or umbilicate in the center of the pileus with the lamellate hymenophore deeply decurrent; or adnate-subdecurrent; sometimes developing HCN; pileus dry or hygrophanous, very rarely viscid, pigmentless or colored, and then pigment intraparietal (often incrusting) and/or intracellular and dissolved in the cell sap, dull colored (gray, umber, etc.), or green, or very frequently ochraceous, pinkish buff, cinnamon, fulvous-chestnut color, etc.; epicutis little differentiated, consisting of a sericeous or subpubescent covering of repent or loosely interwoven filamentous hyphae, rarely cellular; lamellae thin, often arcuate, white, concolorous with the pileus, or cream colored, mostly rather close and narrow; spore print pure white, cream color, greenish, or pale sordid salmon color (but never pale vinaceous drab) spore wall always smooth under the light microscope (but see pl. 46, fig. 6-7), acyanophilic or more rarely slightly cyanophilic; always inamyloid, very thin;

\* This species is obligatory for *Clitocybe* Kummer. Also for those who cite *Clitocybe* (Fr.) Staude or (Fr.) Kummer (but see *Mycologia* 47: 147-149. 1955 and 270-272. 1955!) the choice *A. infundibuliformis* = *gibbus* is the correct one (both species were proposed by Clements & Shear 1931, Singer 1936 and others whereas Earle and Murrill merely indicated what they considered proper according to the principles of the nomenclatorial code they accepted). *C. nebularis* corresponds less well to the original diagnosis having yellowish spores and neither strongly declivous nor infundibuliform pileus, shapes which alone justify the tribus-name. Fries (1838, p. 55) says: "fungi...ut plurimum plano-depressi l. infundibuliformes" which, taken together, cannot but suggest that the word *clitos* is here used for a slope against the middle of the pileus. Fries did not believe that all spore prints in *Clitocybe* are white (see for example *A. hirneolus*, Fries, l.c., p. 58). The present case is not comparable with that of *Pleurotus* where the name is conserved. Thus, Donk's suggestion of *A. nebularis* as type species is not acceptable.

Bigelow (1982) while agreeing with regard to the rejection of *C. nebularis*, proposes *C. clavipes* as type species of *Clitocybe* because *A. gibbus* is not part of the subsection *Genuini* of sect. *Dasyphylli* Fr. of tribus *Clitocybe* in 1821. However, at that time, *Clitocybe* was based on nine sections, with the basionyms "Tereticaul. sp. Scop. p. 429. Gymnop. & Omphal. spec. Pers. Syn...." and no type group for that tribus was indicated but could (implicite) be any of the species indicated by Persoon including *A. gibbus* (p. 449 of *Synopsis*). This was corrected in *Elenchus Fungorum I* which for nomenclatorial purposes is considered to be part of *Systema*, with the words "Here, we offer a more natural series", and the *Genuini* have now disappeared, and with them *A. clavipes*! If, then, we want to respect the Friesian tradition, and Fries's developing ideas as expressed in the starting point work, we cannot accept any but the first species proposed as lectotype (Clements & Shear 1931, Singer 1936) - a choice which must be followed (Art. 8.1), particularly if we quote *Clitocybe* Kummer rather than (Fr.) Staude. But whatever the author citation, the shape of the pileus and the omission of "*Genuini*" and *A. clavipes* in *Elenchus I* make *A. clavipes* a choice that cannot be recommended with a view at the Guide for the determination of types (Code 1978 p. 75-76).

basidia normal, usually 4-spored; cystidia most frequently none, but in some species (mostly scarcely pigmented) cheilo- and/or pleurocystidia are present, also occasionally pseudocystidia; hymenophoral trama mostly regular, often of the *Clitocybe*-subtype, more rarely subirregular, especially in age, not bilateral (excepting the primordia), nor strongly intermixed or inverse; not gelatinous; trama monomitic, neither with distinct gelatinized zones (except sometimes in the spicutis) nor reviving after dehydration, context of the pileus not though or leathery; stipe usually central, but in a few species eccentric to almost lateral, solid or becoming hollow, but generally neither cartilaginous nor extremely thin and fragile, its context fleshy and soft or fibrous and rather hard and elastic; clamp connections in the carpophore generally numerous, in few species scarce or absent (sect. *Disciformes*); hyphae inamyloid, in places with somewhat thickened wall, but often all thin-walled. Urea accumulation in carpophores generally high. On soil, humus, and rotten wood, on foliage and needles, in and outside the woods from the lowlands to the alpine region, rarely on charcoal, dung, on desert sands, in deep moss etc.

*Development of the carpophores:* Probably mostly gymnocarpous, but in *C. geotropa* gymnangiocarpous and stipitocarpic according to Reijnders.

*Area:* Nearly cosmopolitan, from the tropics to the arctic; in all continents excepting Antarctica.

*Limits:* The delimitation is easy with regard to the preceding genera. *Lepista* which has been made a section of *Clitocybe* by Bigelow & Smith (1969) differs clearly by minutely rough to verruculose spores; their ornamentation is strongly cyanophilous whereas in all species of *Clitocybe*, even in those with pinkish or yellow spore print, the spores are smooth under oil immersion lens, not or rather weakly and quite evenly cyanophilous (e.gr. *C. marginella* Harm.). About a third of the species of *Lepista* are tricholomatoid and have violet and lilac intracellular pigments which are foreign to *Clitocybe*. If *Lepista* is incorporated in *Clitocybe* it becomes unavoidable to include also *Tricholoma* subgenus *Contextocutis*, and - why not? - the omphaloid genera *Omphalina* and *Gerronema*. This corresponds to the originally very wide genus concept of Bigelow which he has partly abandoned since 1970. The difference between *Lepista* and *Clitocybe* is sharp enough, and there can be no claim that a gradual "transition" leads from one taxon into the other. Such apparently intermediate species as *C. highlandensis* are obviously in need of further study; the spore ornamentation, visible only under the scanning microscope, has not been checked for cyanophily, and the absence of clamp connections sets it apart at any rate. Other species like *C. leucopaxilloides* Bigelow & Smith are by no means either *Clitocybe* or *Lepista* or even *Clitocybinae*, and should not have been inserted in *Lepista*. On the other hand, the present author (1951, 1962) has undoubtedly contributed to the difficulties of delimitation by leaving the section *Eulepistae* in *Clitocybe*. This problem has been thoroughly restudied, and I agree with Bigelow & Smith and Harmaja that this so-called section of *Clitocybe* should be reunited with the other species of *Lepista*.

If *Lepista* is recognized as a separate genus, it is easy to separate the clamped Tricholomas from *Clitocybe*. They differ by combining typical tricholomatoid habit

with white spore print, and their spores appear smooth even under the scanning microscope (cf. Pegler & Young, 1971, pl. 5, fig. 1).

But the delimitation of *Clitocybe* from *Omphalina* and *Gerronema* requires some comment. With regard to *Gerronema* (which Bigelow calls *Omphalina*), I am in agreement with Bigelow (1970) who stated that the erection of the genus *Gerronema* based on differences in pigmentation mainly, was a step in the right direction. Unfortunately, the type species of *Omphalina* was misinterpreted by Bigelow; some species not belonging in the genus were admitted and others definitely inseparable from the rest, like *G. fibula* were excluded. The present author (1948) has also erred by recognizing a section *Umbilicatae* in *Clitocybe* rather than in *Gerronema* - mainly because the genus *Gerronema* had not been fully known and evaluated before 1964. Yet, the delimitation from *Gerronema* can be achieved much on the same basis as suggested by Bigelow who says that the small species of *Clitocybe* differ by their pigment, which may be emended by pointing out that the small hygrophanous and dirty colored or gray *Clitocybes* have intraparietal pigment whereas the corresponding *Gerronemas* have only intracellular pigment. The bright yellow and orange (often carotenoid) pigments found in *Gerronema* do not occur in *Clitocybe*. The quantity of urea accumulation also separates *Clitocybe* from *Gerronema*, but with few species analyzed, we do not know how constant this difference is.

Bigelow thinks that the species classified by me and most other mycologists in *Omphalina* are more closely related to *Clitocybe* because of the incrusting pigments. Whether closer or less close than *Gerronema*, these species differ from *Clitocybe* by being strictly omphaloid (it is from them that the term omphaloid was taken). Harmaja (1969) discusses in his excellent paper on the genus *Clitocybe* the relation of the latter to *Omphalina*, and comes to the conclusion that for many reasons (spore size, abundance of incrusting pigment, physiological and ecological characteristics) *Omphalina* can well be separated from *Clitocybe*, particularly the smaller species. This should include the fact that there is a general tendency in *Omphalina* to form parthenogenetic and clampless forms, and to be associated with algae to form basidiolichens. Altogether, the key characters as given in the key to the genera, are valid and should not lead to generic misdeterminations.

While there is full agreement with Harmaja, there is only partial disagreement with Bigelow. Bigelow's data which I have amply discussed with him, for which I am truly grateful, have, together with his publications, contributed to a better understanding of the taxonomic situation. The disagreements left are minor - in part referring to nomenclatorial questions, in part to the delimitation in detail of three genera involved. For further comments on these remaining details, I refer also to the discussion of the delimitation of the genera *Gerronema* (p. 274. As for the limits between *Clitocybe* and *Armillariella*, see the latter genus.

With regard to the delimitation of *Clitocybe* and genera not belonging to the Tricholomataceae, we have to discuss three aspects (1) the relation of *Clitocybe* and *Pleurotus*, (2) the relation of *Clitocybe* and *Hygroaster*, (3) the relation of *Clitocybe* and other Tricholomataceae, particularly *Neoclitocybe*.

1. There is a group of species which I now consider to belong to *Clitocybe* in which we have eccentric stipes, frequently small pleurocystidia, frequently lignicolous habitat and slightly to distinctly thickened hyphal walls. Harmaja (1969) and Corner (1980) seem to think that *C. lignatilis* belongs, with *Pleurotus*, rather in the Polyporaceae-complex, because of the partly thickened hyphal walls and the wood-inhabiting mycelium. However, we have truly centrally stipitate species with throughout thin hyphal walls like *C. truncicola*, a species which is constantly lignicolous and acystidiate, obviously closely related to *C. dealbata*. On the other hand, I as well as other authors have observed trama hyphae with slightly but not persistently thickened walls (walls up to 0.8 µm thick) in several typical terricolous *Clitocybes* e.gr. *C. spodoxutha*, *C. melliolens* et al.). The hyphal walls of *C. lignatilis* (in the sense of Pilát, det. Pilát) which I have restudied with particular care, are not really thick-walled, even in mature specimens where the hyphae are often densely agglutinated which makes the walls appear thick, but I measured them as being 0.2-0.8 µm thick, i.e. not thicker than in other non-lignicolous, centrally stipitate forms. These hyphae are often very irregularly inflated in the hymenophoral trama, but even though not quite parallel in mature specimens, strictly axially arranged, and forming a subregular structure. Such a trama is not comparable to that of *Pleurotus*, and in *Lentinus*, characterized by regular trama, this species has not the slightest affinity. It is true that some *Clitocybes*, and not only the lignicolous ones, have elongated, oblong to fusiform spores, but this alone does not make them polyporaceous inasmuch as strictly related forms of the stirps *C. lignatilis*, particularly tropical ones, have short spores (including *C. lignatilis*). It is also true that the lignicolous pleurotoid *Clitocybes* sometimes have cystidia or pseudocystidia, but these are of an entirely different type as compared with the (mostly metuloid) cystidia of the Polyporaceae, and their hymenophoral trama is different from that of *Pleurotus*. The pleurotoid, lignicolous, white *Clitocybes* can therefore be distinguished from *Pleurotus* by regular to subregular hymenophoral trama and in most cases by the shape of the spores and less thick-walled to thin-walled hyphae, the cystidiate ones by different types of cystidia. They differ from such species as *Pleurotus eugrammus* in white instead of violet spore print. They differ from *Lentinus* either in clitocyboid habit or in uninucleate spores or both.

2. The question of *Hygroaster* has already been discussed under Hygrophoraceae. If the genus were transferred to the Tricholomataceae, it would indeed key out in the Tricholomataceae, but differs from both *Clitocybe* and *Omphalina* by the stellate spores, from *Clitocybe* also by the absence of clamp connections, the structure of the trama, and other characters.

3. Among the other Tricholomataceae, *Clitocybe* is similar and related to *Neoclitocybe* to such a degree that the distinction is not always easy or immediate, and often requires careful anatomical study. Not all *Neoclitocybes* have insititious stipe, and not all of them have a very well developed *Rameales*-structure; but the presence of either one of these characters, or revivescent carpophores, or strictly omphaloid habit clearly relates to *Neoclitocybe*. Likewise, the presence of nodulose or branched cheilocystidia and fusoid basidioles indicates *Neoclitocybe*, and not *Clitocybe*. Certainly, the affinity of *Neoclitocybe* is closer to *Marasmiellus* than to

*Clitocybe*, and the geographic distribution of the species is also much more like that of *Marasmiellus*. *Trogia*, also belonging to the affinity of *Neoclitocybe* differs from *Clitocybe* by toughish consistency, a basal socle, and an epicuticular trichodermium. *Trogias* are lignicolous and more or less reviving after desiccation. See also p. 308.

4. *Clitocybe* has occasionally been extended to accomodate such genera as *Hygrophoropsis* and *Cantharellula* and related genera of the Leucopaxilleae. *Hygrophoropsis*, as we now know has not always pseudoamyloid spores, but the spores are constantly strongly cyanophilous, much more so than any *Clitocybe*-spores. In addition, the trama is throughout remarkably soft-fleshy with almost subgelatinized hyphae as in boletes and the pigments are different from those occurring in *Clitocybe*, even in their chemical constitution. The repeatedly forked lamellae are occasionally also found in the Tricholomataceae, but here mainly in genera with amyloid spores. Amyloid spores are not found in *Clitocybe*, but they are characteristic for clitocyboid Leucopaxilleae. Kühner (1980) believes that these smooth-spored Leucopaxilli are indeed more closely related to certain species of *Clitocybe* than to *Leucopaxillus* and called my classification of the amyloid-spored Tricholomas and Clitocytes "artificielle". While this may be so, it must be remembered that (1) it was Kühner himself who first generically separated *L. lepistoides* from both *Tricholoma* and *Clitocybe*; (2) that the smooth-spored Leucopaxilleae are as closely related to each other and to *Leucopaxillus* as they are to inamyloid-spored genera and that Kühner did not prove otherwise in his long discussion of these fungi, treating many of them merely on the basis of literature data. Since Kühner does not know *Porpoloma* subgen. *Porpoloma* and *L. septentrionalis* and *L. sainii* Sing. ined.\*, it escaped him that (1) the three smooth-spored Leucopaxilli form a perfect series from tricholomatoid-sinuate lamellae to decurrent lamellae (*L. septentrionalis* - *L. lepistoides* - *L. giganteus* + *L. candidus*). For *L. lepistoides* Maire described the lamellae as "sinuate-adnate or a little decurrent, then often adnate-emarginate", and Kühner himself indicated as characteristic for *Leucopaxillus* that "one observes all transitions from tricholomatoid to clitocyboid forms" (p. 266). (2) The typical Porpolomas have cheilocystidia making the edge heteromorphic and never have gigantic carpophores nor readily separable hymenophore with the lamellae not rib- or dent-like decurrent. This section *Aspropaxilli* is transferred to *Clitocybe* with inclusion of species with non-amylid spores (our section *Disciformes*) by Bigelow who, however, separates the *L. giganteus* group in a special subsection. This is in contrast to Kühner who approximates *Aspropaxillus* to *Clitocybe geotropa* and *C. maxima* which according to Bigelow belong in a different subgenus "*Infundibuliformes*" (our section *Clitocybe*, not Bigelow's). In neither case do we see any close relationship since in the section *Disciformes* the shape of the carpophores, especially the pileus (eventually shallowly depressed) is different from the more clitocyboid shape of the carpophores in the species *L. giganteus* and *L. candidus* whereas in the section

\*This species, from India, is very similar to *L. giganteus* but has cheilocystidia of the kind observed in sect. *Leucopaxillus*.

*Clitocybe (Infundibuliformes)* the spore shape and size and/or the epicutis structure and pigment localization are different from that in the *Leucopaxilli*. Furthermore, the difference in lamellae attachment is so small (and fluent) among the species of the otherwise so similar species of *Aspropaxillus* that it is impossible to separate them from each other by that one character and distribute them in different genera, as Kühner suggests. The amyloidity of the spores, even if slight or weak, or not affecting all spores of a dried specimen, is a sharp and decisive character, and will serve perfectly well to differentiate *Clitocybe* from *Leucopaxillus* (and the Leucopaxilleae), even if the tribus Leucopaxilleae remains just possibly artificial (cf. p. 288, 297).

*State of knowledge:* The genus *Clitocybe* is very rich in species. Relatively few species have been checked for chemical and physical characters now obviously useful in the taxonomy of the genus. Harmaja (1969) has very thoroughly studied the species occurring in Finland and adjacent regions and has used a new approach by emphasizing the action of ultraviolet light on dried specimens and the tendency of the spores to adhere to each other in tetrads, the shape of the hilar end of the spores, some chemical characters, and the pigment localization. Bigelow (in various papers) has studied most of the American species in some detail, and the neotropical species have for the first time been studied by Singer who also published a key to the species (*Sydowia* 31: 199-233. 1978). Unfortunately, modern data are not available for all species which might be considered as "good"; therefore the enumeration given below is far from complete (115 species).

*Practical importance:* Some species are good edible fungi; others are poisonous, causing disease with the characteristic muscarine syndrome (the presence of muscarine has been reported by Genest, Hughes & Rice, *Journ. Pharm. Sc.* 57: 331-333. 1968) in the *C. dealbata* group and *C. hydrogramma*; it is certain that these species contain muscarine. Another poisonous species according to its author, *C. venenata* Heim (*Cah. Makobé* 4: 85-90. 1966) is unknown to me. As in other genera, the presence of alkaloids is often accompanied by antibacterial activity. Muscarine isomeres were also observed by Stadelmann et al. in *C. gibba* - a species generally believed to be edible - and in *C. vermicularis* (apparently the species here indicated as *C. rhizophora*.) Diatretine 2, often found in *Clitocybe*, has antibiotic properties (Anke, *Zeitschr. f. Mykol.* 44: 130. 1978). Nebularine from *C. nebularis* is bacteriostatic (Loefgren et al., *Acta Chem. Scand.* 8: 670-680. 1954). *C. clavipes* has been found to cause mild poisoning when ingestion is followed by alcoholic drinks (Cochran K.W. & M.W., *Mycologia* 70: 1124. 1978).

## SPECIES

Subgenus I. **Clitocybe** (*Eu-Clitocybe* Konr. & Maubl. 1924-37). Pileus fleshy; if hygrophanous, rhizoid-like pseudorrhizas are extremely abundant, or an odor of anise or *Collybia dryophila* is distinct, or else the whole fruiting body is more or less pigment-less or the pileus cinnamon-flesh-color; if the pileus is hygrophanous and dull colored, the pigment is not incrusting or intraparietal. Spore print white or

variously colored; hyphae, especially in and near the epicutis, not vesiculosely widened and epicutis never subhymeniform; cystidia and cheilocystidia none or the latter very rare and inconspicuous.

*Type species:* *C. gibba* (Pers. ex Fr.) Kummer = *C. infundibuliformis* (Schaeff. ex Fr.) Quél.

Sect. 1. *DISCIFORMES* (Fr.) Quél. (1872). Pileus often very large, generally convex to planate and even if often becoming shallowly depressed in age but rather convex at beginning maturity; young lamellae often merely adnate or even sinuate, old lamellae often separable from the context of the pileus, subdecurrent or decurrent; spore print most frequently pure white to cream or ochraceous, or flesh-pink to cream-salmon; pileus always well pigmented if spore print white; pileus not hygrophanous (not even partially) unless the spore print is colored and/or with protocarp-like basal bulb, without distinct incrusting pigment. Surface of pileus dry or moist, rarely viscid or hygrophanous; frequently with a greenish pigment; clamp connections present, sometimes extremely rare or even absent.

*Type species:* *C. nebularis* (Batsch ex Fr.) Kummer.

Subsection *Clavipedes* (Harmaja) Sing. (1973). Spore print white; clamp connections present, rarely rare or even absent; surface of pileus, viscid or dry, glabrous or pruinose or finely (under a lens) tomentose; spores small to medium sized, ellipsoid with rounded base (or at least many spores with rounded base present); odor not of anise; lamellae decurrent to subdecurrent, rarely sinuate; colors never greenish but gray, brownish or brown, fuscous, rarely with an olive shade, sometimes without pigment. Surface of pileus often unevenly colored or uneven because of warty, tomentose, or silvery spots or areas.

*Type species:* *C. clavipes* (Fr.) Kummer.

*C. clavipes* (Fr.) Kummer; *C. alexandri* (Gillet) Konrad sensu Bigelow (an Harmaja\*; *C. crassa* Bigelow & Smith; *C. harperi* Murr.; *C. espinosae* Sing.; *C. columbiana* Sing.; probably also *S. subsimilis* Peck).

Subsection *Inornatinae* Sing. (1948). Spore print (where known) white or barely off white; spores strongly elongated, oblong to fusiform; carpophores sometimes rising from a fleshy mass (parasitic?).

*Type species:* *C. inornata* (Sow. ex Fr.) Gillet.

*C. inornata* (Sow. ex Fr.) Gillet; *C. avellanea* (Murr.) Sing.; *C. chudacea* Maire; *C. avellanea* *alba* Murr.; *C. mexicana* Murr.; *C. lata* (Peck) Sing.; *C. sclerotoidea* (Morse) Bigelow; obviously also *C. umbrinipes* Bigelow (unless = *C. inornata*).

Subsection *Subuliferae* Sing. (1961). Differing from the preceding section in the presence of cystidia which are mostly subulate. Spore print white. Clamp connections present.

\*There is in this species an intercellular pigment observed in most dried specimens and reported by Harmaja. This might be a necropigment according to Kühner (1980, p. 307).

*Type* and only species: *C. subulifera* Sing.

Subsection *Nebularinae* Sing. (1948). Spore print ochraceous or ochraceous cream ("ivory yellow" Ridgway or "C" Crawshay or 9-G-1/2 M & P). Pileus either white or gray to buff gray, brown gray, without greenish tinges; spores elliptical, some somewhat oblong, medium sized (6-9  $\mu\text{m}$ ), their walls often  $\pm$  cyanophilic (but in contrast to those of *Lepista* uniformly and rather weakly so); dried specimens showing a chloric-greenish or yellow fluorescence in all parts (including the basal mycelium) under ultraviolet light (in contrast to other species investigated in this section); odor not of anise.

*Type species*: *C. nebularis* (Batsch ex Fr.) Kummer.

*C. robusta* Peck (*C. alba* (Bat.) Sing.); *C. nebularis* (Batsch ex Fr.) Kummer.

Subsection *Odorae* (Bigelow 1982 p. 148 ut sectio) Sing. Spore print pink, pure white, or with a greenish shade; spores medium sized (6-8  $\mu\text{m}$ ); clamp connections present; color mostly with some greenish tinge on the pileus which is not or scarcely hygrophanous and not viscid. Odor often of anise.

*Type species*: *C. odora* (Bull. ex Fr.) Kummer.

*C. odora* (Bull. ex Fr.) Kummer; *C. trogii* (Fr.) Sacc.; *C. aeruginea* Bigelow; *C. glaucoalba* (Sing.) Sing. - The last two species with white spore print might be separated to form another subsection.

Subsection *Pruinatae* Harmaja (1969). Spore print salmon-pink, cream-pink, pink; spores small (4-6  $\mu\text{m}$ ); clamp connections present; color never greenish; pileus hygrophanous or not, not viscid; odor never of anise.

*Type species*: *C. phyllophila* (Fr.) Kummer.

*P. martiorum* Favre; *C. phyllophila* (Fr.) Kummer; *C. marginella* Harmaja; *C. diatreta* (Fr.) Kummer.

Sect. 2. *CLITOCYBE* (*Infundibuliformes* (Fr.) Quél.). Pileus soon depressed to infundibuliform, pale buff or fulvous, pinkish buff to chestnut, red-brown to brownish orange, never hygrophanous and never viscid; lamellae deeply decurrent almost from the beginning; stipe without rhizoid mycelial fibrils (white rhizomorphs) or with few inconspicuous ones; spore print never ochraceous or pink, but sometimes reaching a yellowish white especially in dehydrated condition (9 B 1 according to Harmaja\* M. & P.); spores of variable size and shape, mostly elliptical to guttiform, ovoid, etc., small to medium sized; mostly (or consistently?) acyanophilic..

*Type species*: *C. gibba* (Pers. ex Fr.) Kummer.

Subsection *Clitocybe*. Spores mostly all tearshaped (base not rounded), small to medium sized; basal tomentum white; odor camphor-like or of HCN, or absent.

\*Bigelow indicates the spores of *C. sinopica* as cream to pale yellowish (fresh?). I find them white. Bigelow's is an undescribed different species according to Harmaja (1969).

*Type species: C. infundibuliformis* (Schaeff. ex Fr.) Quél. = *C. gibba*.

*C. bresadolanoaffinis* Sing.; *C. bresadoliana* Sing.; *C. gibba* (Pers. ex Fr.) (C. infundibuliformis (Schaeff. ex Fr.) Quél.; *Agaricus*, Schaeff. ex Fr. non Bull. ex St-Amans); *C. flaccida* (Sow. ex Fr.) Kummer non al. (*A suavis* Pers. 1822 non 1828); *C. altaica* Sing.; *C. costata* Kühn. & Romagnesi (if not too close to the preceding species); *C. squamulosa* (Pers. ex Fr.) Kummer; *C. catinus* (Fr.) Quél.; *C. maxima* (Fl. Wett. ex Fr.) Kummer; *C. geotropa* (Bull. ex St-Amans); *C. splendoides* Bigelow (*C. splendens* (Fr.) Quél. sensu Bres. non al.); obviously also *C. lateritia* Favre, *C. rubella* Bigelow (rising from a "sclerotoid" mass as *C. sclerotoidea*), and *C. paropsis* (Fr.) Quél. (sensu Bresadola, Lamoure); probably also *C. calcarea* Velen. (possibly subsection *Gilvaoideae*).

Subsection *Gilvaoideae* (Harmaja) Sing. (1973). Both spores with broad base and tear-shaped spores present, small (4-6 µm); basal tomentum not white; odor none, or farinaceous; hyphae of epicutis smooth.

*Type species: C. gilvaooides* Kauffm.; obviously also *C. gracilis* (Bigelow & Sm. apud Bigelow) Harmaja.

Subsection *Sinopicae* (Harmaja) Sing. (1973). Spores with broad base or mixed, medium sized (to 11.5 µm, mostly 6.5-10 µm long); basal tomentum white; odor often strong.

*Type species: C. sinopica* (Fr.) Kummer.

*C. sinopica* (Fr.) Kummer; obviously also *C. incisa* Bigelow (unless too close to the preceding species), *C. incilis* (Fr.) Quél. (sensu Favre), and *C. squamuloides* Orton (1961) (*A. cimicarius* Pers., type).

Sect. 3. *CANDICANTES* (Quél.) Konr. & Maubl. (1948). Spore print as in the preceding section. Pileus hygrophanous in age only, or hygrophanous from the beginning, either white or, if hygrophanous, with some dull grayish-straw or dull cinnamon to sordid cream shades when wet and then spores small (up to 6 µm), usually a high percentage agglutinated in tetrads (Harmaja); pigments not intraparietal and lamellae at first not gray (later sometimes darkening).

*Type species: C. candicans* (Pers. ex Fr.) Kummer.

*C. candicans* (Fr.) Kummer, var. *candicans* and var. *dryadicola* (Favre) Lamoure; *C. cerussata* (Fr.) Kummer; *C. angustissima* (Lasch) Kummer; *C. regularis* Peck (if not too close to the three preceding species); *C. laricicola* Sing.; *C. catalaunica* Sing.; *C. nothofageti* Sing.; *C. leptoloma* (Peck) Peck; *C. subleptoloma* Sing.; *C. melliolens* Sing.; *C. spodoxutha* Sing.; *C. subhygrophana* Sing.; *C. subhygrophanoides* Sing.; *C. robinsoniae* Murr.; *C. truncicola* (Peck) Sacc.; *C. augeana* (Mont.) Sacc.; *C. dealbata* (Sow. ex Fr.) Gillet\*; *C. rivulosa* (Pers. ex Fr.) Kummer

\*The *C. dealbata* of C.H. Kauffman is *C. truncicola*; *C. sudorifica* and *C. morbifera* are *C. dealbata*; *C. corda* Schulz is apparently a variety of *C. dealbata* but is said to be identical with *C. rivulosa* (according to Bohus).

(if not merely a variety of *C. dealbata*); *C. subbulbipes* Murr.; here also *C. brumalis* (Fr.) Quél. in the sense of certain authors and *C. asema* Sing. (*C. brumalis* sensu Sing. & Digilio).

Note: Other species formerly inserted here by me are in need of further study: *C. washingtoniensis* Murr. (possibly identical with or close to *C. phyllophila*), *C. setiseda* (Schwein.) Sacc.; *C. steppicola* Sing.; *C. ericetorum* Quél. sensu Lange; *C. tuba* (Fr.) Gillet; *C. griseifolia* Murr. (considered close to *C. harperi*, sect. 1, by Bigelow); apparently also *C. luffi* (Mass.) Orton, "*Omphalia*" *microspora* Bres., and *C. microspora* Peck.

The entire group with fragrant, marzipan or anise-like odor is likewise added here: *C. suaveolens* (Schum. ex Fr.) Kummer (sensu Fries 1821); *C. fragrans* (With. ex Fr.) Kummer (sensu Bigelow); *C. obsoleta* (Batsch ex Fr.) Quél. sensu Moser, Bigelow; *C. marthae* Sing.; *C. patagonica* Sing.; *C. subhygrophanoides* Sing. - All these have anise-like or marzipan-like odor and supposedly white spore print. Those with salmon colored spore print see section 1. However *C. fragrans* (Sow. ex Fr.) Kummer has been re-interpreted in such a manner that it does not fit the diagnosis of the present section because of the presence of intraparietal pigment, and spore print 9 B 2 (M. & P.) according to Harmaja (whereas *C. suaveolens* in our sense has white spore print and spores with broadly rounded base); this is *C. fragrans* sensu Harmaja, see subgenus II.

Sect. 4. *VERNAE* Sing. (1943). Differs from the preceding sections in the base of the stipe showing an abundance of "rhizoids", i.e. white rhizomorphs. Fresh spore print white to cream white (i.e. Romagnesi Ia-Ib); pileus more or less hygrophanous; pigments intracellular.

Type species: *C. rhizophora* Velen.

*C. rhizophora* Velen.; *C. radicellata* God. in Gillet (*C. pruinosa* (Lasch) Kummer sensu Harmaja); *C. autumnalis* Sing.; *C. rhizoides* Bigelow & Sm. (but identical with *C. radicellata* according to Harmaja); probably *C. alborrhiza* Bigelow & Sm. (although inserted in sect. 1 by its authors) and *C. basirosea* (Rick) Sing.

Sect. 5. *LIGNATILES* (Konr. & Maubl.) Sing. (1972). Differs from sect. 3 and the other sections of subgenus *Clitocybe* by eccentric to almost lateral stipe, i.e. pleurotoid habit, at least in most specimens of a group. Pileus white and slightly to distinctly hygrophanous. Cystidia none. No intraparietal pigment.

Type species: *C. lignatilis* (Pers. ex Fr.) Karst.

*C. lignatilis* (Pers. ex Fr.) Karst.; *C. pleurotus* Sing.; *C. kabulensis* Sing. (*Pleurotus komarnitzkyi* Vasilkov?); *C. josserandii* Sing.

Sect. 6. *ABERRANTISSIMAE* Sing. (1961). Pigment absent or pale buff; stipe central to ± eccentric and from somewhat oblique to strongly curved; cheilocystidia and usually also pleurocystidia present, these often not very conspicuous and mostly filiform with somewhat widened basal portion, thin-walled, without contents visible in KOH mounts, hyaline, or pseudocystidial with inner outline of the wall not discernible and with granular contents in KOH.

*Type species: C. aberrantissima* Sing.

*C. scandens* Sing.; *C. aberrantissima* Sing.; *C. lignicola* Sing.; *C. fimbriata* Sing.

**Subgenus II. *Pseudolyophyllum*** Sing. (1943). Pileus hygrophanous, neither greenish nor otherwise bright colored, pigment often intraparietal or incrusting, always so if the pileus is pale colored or viscid; stipe fleshy and solid, central, with basal mycelium but generally without conspicuous white rhizomorphs. Hyphae not abruptly widened into ampullaceous or vesiculose cells with contents although they may be rather strongly inflated with narrowed diameter at the septa; epicutis never subhymeniform; odor not of anise; cystidia none.

**Sect. 7. *PSEUDOLYOPHYLLUM*.** Habit clitocyboid but young carpophore at times appearing tricholomatoid; spores small to medium sized and ellipsoid with rounded-obtuse base; spore print white. Mostly growing in coniferous woods of the temperate zones. Pileus never viscid. Odor and taste typically not farinaceous.

*Type species: C. metachroa* (Fr.) Kummer.

*C. metachroa* (Fr.) Kummer; *C. metachroides* Harmaja.

Note: Harmaja has, probably correctly so, emended this section so as to exclude all species with the characterization of section 8, *Ditopae*, i.e. those which have lamellae violet in ultraviolet light, or which have farinaceous odor and dried concentrically wrinkled pileus; the following species are inserted here on a temporary basis pending a more detailed study, especially with regard to the pigment localization in fresh specimens.

*C. expallens* (Pers. ex Fr.) Kummer (sensu Bresadola) (possibly better in *Gerronema*); *C. vibecina* (Fr.) Quél. (sensu Bres.); *C. langei* Sing. ex Hora\*; *C. decembris* Sing.; *C. pseudoobbata* Lange; *C. concava* (Scop. ex Fr.) Gillet (sensu Lamoure who tentatively identifies this species with *C. strigosa*, the type of section *Strigipedes*, see below); *C. imaina* Sing.; *C. fuligineipes* Metrod; *C. obscuratipes* Sing.; *C. pausiaca* (Fr.) Gillet (*C. foetens* Melot); *C. lituus* (Fr.) Métrod ("litua").

**Sect. 8 DITOPAE** Sing. (1948). Spores typically small and broad, otherwise like section 7 (but according to Harmaja lamellae of dried specimens in this section 9 violet in ultraviolet light, odor and taste farinaceous; pileus dried concentrically wrinkled and spores in some species also ellipsoid and larger).

*Type species: C. ditopa* (Fr.) Gillet; *C. brunnescens* Murr.; *C. murinifolia* Murr. (possibly all three identical)

Note: I doubt whether species like *C. orientalis* Harmaja with elongated spores could enter here (but do not know that species). Neither am I familiar with the species Harmaja (1969) puts in his new sections *Latisporae* and *Strigipedes* with the exception of *C. strigosa* Harmaja unless this is indeed the same as *C. concava*, which is here tentatively inserted in section 7. *C. crispa* Bigelow & Sm. obviously belongs in

\*As correctly stated by Harmaja (1969), my *C. langei nomen subnudum* differs from *C. langei* Hora. My species has no farinaceous odor or taste. Kühner & Romagnesi's and Hora's has.

section *Strigipedes* if the latter is accepted as different from sect. *Pseudolyophyl-lum*.

Sect. 9. *FRAGRANS* (Harmaja) Sing. (*Lepista* sect. *Fragrans* Harmaja, *Karstenia* 18: 53. 1978). Differs from sect. 7 in pale pinkish-salmon spore print (9 B 2, Maerz & Paul); odor distinctive; lamellae adnate to subdecurrent, not deeply decurrent; epicutis and hypodermium without incrusting but the latter with intraparietal pigment; pileus sometimes becoming deeply depressed, but rather small and thin.

*Type species:* *L. fragrans* sensu Harmaja (*C. harmajae* Lamoure).

*C. harmajae* Lamoure; probably also *C. deceptiva* Bigelow.

Sect. 10. *FARINOENTES* (Sing.) Sing. 1961. Differs from section 9 in collybioid to vaguely omphalioid habit and  $\pm$  gelatinized epicutis, constantly incrusting pigment and gray FeSO<sub>4</sub> reaction. Odor and taste farinaceous. Lamellae adnate to decurrent. Generally growing outside the forested areas or accidentally under trees.

*Type species:* *C. vulgaris* Sing.

*C. vulgaris* Sing. (synonym of *C. fellea* Peck acc. to Bigelow); *C. barbularum* (Romagnesi) Orton; probably also *Collybia expallens* Peck.

Subgenus III. *Cystoclitus* Sing. (1955). Epicutis of pileus containing numerous swollen elements, these gradually or abruptly inflated, often containing a remarkable internal body of unknown constitution; these inflated bodies reaching a diameter of up to 9 times that of the uninflated hyphae, and in some species become so dense that they form a subhymeniform epicutis. White or dull-colored.

Sect. 11. *BULLULIFERA* Sing. (1943). Epicutis not subhymeniform. Species of the Northern Hemisphere.

*Type species:* *C. hydrogramma* (Bull. ex Fr.) Kummer.

*C. hydrogramma* (Bull. ex Fr.) Kummer; also *C. adirondackensis* (Peck) Sacc. and *C. jalapensis* Murr. (unless too close to the type species).

Sect. 12. *CYSTOCLITUS* Sing. (1962). Swollen elements combining into a subhymeniform epicutis. Species of the Southern Hemisphere.

*Type species:* *C. praeandina* Sing.

*C. podocarpi* (Sing.) Sing.; *C. praeandina* Sing.

## 25. **LEPISTA** (Fr.) W.G. Smith

*Clavis Agar.*, p. 26. 1870.

*Type species:* *Paxillus lepista* Fr.\* [= *Rhodopaxillus densifolia* Favre = *Lepista subaequalis* (?Britz.) (Sing.)].

\*The status of *Paxillus lepista* Fr. as the type species of *Lepista* (Fr.) W.G. Smith is unchallenged. Only Bigelow & Smith (1969) say that "it is not acceptable as a lectotype for a genus". Whatever this statement is supposed to mean, it is nomenclatorially erroneous and apparently based on some remarks by Donk

*Syn.: Paxillus*, trib. *Lepista*, Fr., *Epicr.*, p. 315. 1838.

*Rhodopaxillus* R. Maire, *Ann. Myc.* 11: 337. 1913 (type: *R. panaeolus*).

**Characters:** Pileus hygrophanous, subhygrophanous, or nonhygrophanous; hymenophore lamellate; lamellae emarginate-sinuate as in *Tricholoma*, or more rarely plainly decurrent, often separable from the context of the pileus from which they are divided by a watery or subcartilaginous line or zone; stipe usually central and fibrous-fleshy; context never tough or reviving; carpophores sometimes aggregated into large cespitose masses, or very densely gregarious in circles ("fairy ring"); spores rather small and coarsely to very minutely roughened (Pl. 47) in outline, inamyloid, thin-walled, sometimes part of the spores smooth but always a certain percentage more or less rough, the ornamentation distinctly cyanophilic on scarcely or not cyanophilic ground, ellipsoid, or short-ellipsoid, or ovoid, rarely ellipsoid-oblong, hyaline sordid pink, dull purplish red or yellow, rarely white pale sordid pink to cream pink in mass (on white paper), e.gr. Séguy 200 in *L. sordida*, between E and G, Crawshay if yellow; basidia normal in every regard; cystidia of any sort absent; hymenophoral trama regular or subregular, all hyphae nonamyloid, with numerous clamp connections; epicutis little differentiated. On the soil, on roadsides, in the woods, on meadows, in parks, in steppes and deserts, on manure heaps in the garden, on compost heaps, etc., ordinarily not on wood.

**Development of the carpophores:** Gymnocarpous.

**Area:** Apparently almost cosmopolitan.

**Limits:** The rule indicated under *Clitocybe*, leaving all species with quite smooth spores and those with weakly and continuously or not cyanophilous spore wall in *Clitocybe*, will take care of the present needs of the taxonomist (see p. 237), if it is understood that the "smooth" spores may be SEM-rough\*.

(who does recognize *A. lepista* as type of *Lepista*). When he says that the original fungus was "likely different" from what Fries so called in *Mon. Hym. Suec.* 2: 115. 1863, it does not mean that the identity of the species as described by Fries in the work from which W.G. Smith took the tribus epithet (*Epicr.* p. 315) is apt to be differently interpreted. Neither can his comment - generally acknowledged - that Ricken interpreted the fungus differently (perhaps according to the 1821 diagnosis) be construed to mean, as Bigelow and Smith put it that "no one today really knows *P. lepista* Fries". The contrary is true. The species was well illustrated by Fries himself and by Bresadola, and was redescribed in detail by Singer (1943) and Horak (1968). The whole complex has been discussed from all angles by Singer & Cléménçon (1973) and the only reason why *A. lepista* does not show up much in the modern literature is the obvious fact that, in *Lepista* the epithet is a tautonym, and had to be replaced by a later synonym. I am fully aware that *A. subaequalis* is a somewhat doubtful synonym but accepted it tentatively until a better documented species was discovered - *Rhodopaxillus densifolia* Favre. It should therefore be well understood that, if Bigelow & Smith reject the genus *Lepista*, they cannot possibly do so on nomenclatorial grounds, but because their genus concept is such that *Clitocybe* sensu lato (which includes also species of *Rhodocybe* and *Omphalina*, species with siderophilous granulation and species without clamp connections) includes the species and sections here separated under *Lepista*. But this is another problem, amply discussed below.

\*According to Pegler & Young (1971) the spores of *Clitocybe* are always smooth under the light microscope and in the species examined by them under the scanning microscope they are also smooth with the exception of those of *C. clavipes* (see their Pl. 3, Fig. 6) which show a slight but constant and uniformly distributed rugosity, but are white in print.

Neither the existence of a white-spored form in the *L. inversa*-group nor the different interpretation of *L. irina* (I have collected and described a smooth-spored species from the Leningrad region which apparently is not identical with the current interpretations and seems to belong in *Tricholoma*) should be cited as indicating "intermediate" forms between *Clitocybe* and *Lepista*. I have carefully restudied all the specimens with pinkish spores found in European herbaria and available to me. As far as they are not obvious misdeterminations, they have at least a large number of asperulate spores and the asperulation although often low, is perfectly visible in a light microscope under oil immersion as well as in the scanning microscope. There can be no doubt but that these species belong in *Lepista* and not in *Clitocybe*.

Care should be taken not to confuse species which belong in *Rhodocybe* or *Asproinocybe* inasmuch as these may sometimes be externally similar to true *Lepistas*. As for the delimitation of these species see under these genera.

Harmaja (1976, 1978) recognizes *Lepista* as an autonomous genus independent from *Clitocybe*, as has recently been done by Kühner, Moser and Baroni as well as in older editions of the present book, but in contrast to the authors named and all the others who recognize it, he emends it in such a way that the sections *Pseudolyophyllum*, part of sect. *Disciformes*, and sect. *Frangans* are transferred from *Clitocybe* to *Lepista*. This strong dismemberment of *Clitocybe* is entirely based on the cyanophily (weak or strong) of the spore walls in those species excluded from *Clitocybe* and transferred to *Lepista* without any regard to other characters. Since, however, Harmaja (1976) states that the spores of *Tricholoma* are likewise cyanophilic (his observations are partly in contradiction with my own, see *Mycologia* 64: 829. 1972), the seemingly clearcut differentiation between *Clitocybe* sensu str. (Harmaja) and *Lepista* is merely gained by unsurmountable difficulties in delimiting *Lepista* from *Tricholoma* (for example: Is *Clitocybe glaucoalba* for Harmaja a *Lepista* or a *Tricholoma*?). Even if this were not so, the (often weak) cyanophily of *Clitocybe* species vs. absence of cyanophily in this genus separates closely related species from each other and cannot, if used as a generic character, avoid to lead to a totally artificial classification.

Bigelow describes in his sect. *Verruculosae* Bigelow & Smith (our genus *Lepista*) a species which is supposed to have weakly amyloid ornamentation and "wood brown" to "Army brown" spore print. If correctly described, this species is not a *Lepista* but a (possibly new?) genus of *Leucopaxilleae* or even some other family.

*State of knowledge:* 31 species are now known to belong in *Lepista*.

*Practical importance:* *Lepista* contains some of the most valuable edible mushrooms, and some of the most promising bacteriostatic organisms among the Agaricales. The best known edible species are: *L. nuda* (also grown in France, and often sold in the markets), *L. personata*, *L. sordida*, *L. rickenii*, *L. caespitosa*, *L. caffrorum* (one of the most important edible mushrooms of the natives of South Africa), *L. lactescens* (one of the widely used edible mushrooms in Indo-China), *L. præmagna*.

## SPECIES

Sect. 1. *LEPISTA* (Panaeoli Sing. ut. sect. generis *Rhodopaxillus*, 1943). Stipe more or less white or pallid or at least paler than the pileus; no violet or lilac pigments in the carpophore visible; habit clitocyboid to tricholomatoid, rarely pleurotoid; spore print not white or yellowish but pinkish cream to salmon.

Type species: *Paxillus lepista* Fr. (*L. densifolia* Favre)

*L. caffrorum* (Kalchbr. & McOvan) Sing.; *L. lactescens* (Pat.) Sing.; *L. praemagna* (Murr.) Sing.; *L. subconnexa* (Murr.) Harmaja (vix sensu Harmaja); *L. caespitosa* (Bres.) Sing. (non C. caespitosa Peck); *L. nimbata* (Batsch ex Secr.) Karst. (*Agaricus paneolus* \**calceolus* Fr.; *Tricholoma panaeolum* Quél.); *L. harperi* (Murr.) Sing. (*Clitocybe brunneocephalia* Bigelow); *L. densifolia* (Favre) Sing. & Cléménçon (*Paxillus lepista* Fr. sensu Fr., Bres. non Ricken); *L. geotropoides* Sing.; *L. rickenii* Sing.; *L. glabella* (Speg.) Sing.; *L. westii* Murr.; *L. muritai* Stevenson (*Rhodocybe*, Horak); *L. subisabellina* (Murr.) Pegler; *L. panaeoliformis* Murr.; *L. munduliformis* (Dennis) Sing.\* *L. antipoda* Stevenson; *L. irina* (Fr.) Bigelow; *L. ricekii* Bon (*L. piperata* Ricek non Stevenson); *L. rhodotooides* Sing. in Pegler; obviously also *L. ovispora* (J.E. Lange) Gulden; *L. pseudoectypa* (M. Lange) Gulden; *L. multiformis* (Rom.) Gulden ("multiforme") (*Clitocybe polygonarum* Laursen).

Sect. 2. *SPONGIOSA* (Fr.) Kühn. (1976) (*Genuinae* Konr. & Maubl. as *Rhodopaxillus*, inval.; *Nuda* Harmaja 1978). Stipe more or less bluish-violet or lilac, pale blue or purplish colored when young and fresh or at least such pigments visible in pileus or lamellae; habit mostly decidedly tricholomatoid in normally developed carpophores; spore print pinkish.

Type species: *L. nuda* (Bull. ex Fr.) Cooke\*\*

*L. nuda* (Bull. ex Fr.) Cooke (*Tricholoma*, Kummer; *Rhodopaxillus*, R. Maire) with var. *nuda* var. *tridentina* (Sing. ut *Rhodopaxillus*) Sing., var. *violaceo-fuscidula* (Sing. ut *Rhodopaxillus*) Sing., var. *lilacina* (Quél. ut *Gyrophila*) Sing.; *L. personata* (Fr. ex Fr.) Cooke (*Tricholoma*, Kummer, *Rhodopaxillus*, Sing.); *L. glaucocana* (Bres.) Sing.; *L. sordida* (Fr.) Sing. (*Tricholoma*, Kummer, *Rhodopaxillus*, Maire, *Clitocybe tarda* Peck, *Clitopilus*, Peck 1901; *Lepista domestica* Murr.); *L. diemii* Sing.; *L. fibrosissima* Sing.; *L. argentina* (Speg.) Sing.

Sect. 3. *GILVA* Harmaja (1978) (*Inversae* Sing. & Clém. 1972, inval.). Carpophore without violet, lilac or purplish pigments; habit clitocyboid; spore print white, or more commonly yellow or pinkish cream; spores usually small, distinctly asperulate, said to have a smooth suprahilar spot ("plage") (according to Bigelow 1982).

Type species: *L. gilva* (Fr.) Roze.

*L. gilva* (Pers. ex Fr.) Roze; *L. inversa* (Scop. ex Fr.) Pat.; *L. lentiginosa* (Fr.) Pegler; *L. ameliae* (Arcangeli) Sing. & Cléménçon.

\*c. n. (*Rhodopaxillus munduliformis* Dennis, *Kew Bull. for 1952*: 489. 1952 (1953?)).

\*\*Kühner's transfer with this type species is legitimate since he considered this a substitute for *Genuina* Konr. & Maubl. by implication and therefore the type species must be the same.

A forth section, which Bigelow (1982) described as a subsection apparently of sect. *Verruculosae* (i.e. *Lepista*) and called *Porcasporae* Bigelow with the type species *Clitocybe praefellea* Murr. from Florida is characterized by slightly thickened, punctate-roughened spore wall which in KOH appears punctate-roughened to reticulate and is hyaline; in Melzer dark (but apparently not reddish), in SEM "irregularly horizontally ridged or bands intermixed with verruculae" forming the ornamentation (Bigelow). I do not know any species of *Lepista* attributable to such a section, but find the description of the spores suggestive of the genus *Phyllobolites*.

## 26. TRICHOLOMOPSIS Sing.

*Schweiz. Zeitschr. Pilzk.* 17: 13 [reprint pagination]. 1939.

*Type species:* *Tricholomopsis rutilans* (Schaeff. ex Fr.) Sing.

*Syn.:* *Megacollybia* Kotl. & Pouz., *Česká Myc.* 26: 220. 1972.

*Characters:* Carpophores with tricholomatoid habit, more rarely clitocyboid, or almost pleurotoid because of the somewhat eccentric stipe observed in certain species; well pigmented with an intracellular pigment, at least the cuticle which is either bright colored (and then sometimes with dark-brown, fuscous, blackish squamulae on top of the pigmented surface of the pileus, and the lamellae and stipe often colored with the same bright - usually yellow - pigment), or only the cuticle of the pileus (dull) colored; pileus more or less fleshy, not infundibuliform, more or less squamulose or fibrillose in all species, the cuticle little differentiated except for the terminal member of the hyphae that make up the fibrils; these terminal hyphae often slightly dermatocystidia-like and sometimes filled with a colored cell sap; hymenophore lamellate; lamellae yellowish or white, emarginate-sinuate as in *Tricholoma*, or adnate to somewhat decurrent as in *Clitocybe*, or merely adnexed as in *Collybia*; spore print pure white (or nearly so) on white paper; spores ellipsoid to globose, with thin, later sometimes slightly thickened walls which are smooth, acyanophilic, inamyloid (yellowish in iodine), or very slightly pseudoamyloid (i.e. a minority of overmature spores, i.e. spores that have rested on the hymenophore for a long time, becoming palest brownish in iodine); basidia normal in all regards; cystidia frequently present but often inconspicuous on the sides of the lamellae; but cheilocystidia very prominent on the edges of the lamellae, large to extremely voluminous but with thin walls and therefore soon collapsing to a degree that in dried material they may escape the attention of the observer; hymenophoral trama regular or subregular, consisting of rather long, sometimes even voluminous hyphae which are strongly interwoven to subparallel; stipe central or somewhat eccentric, fibrous-fleshy, solid or stuffed, sooner or later becoming hollow, but never cartilaginous-tubulose; all hyphae inamyloid, with numerous clamp connections. On rather fresh or decayed or buried wood, rarely terrestrial and then often with long white rhizomorphs (sect. *Platyphyllae*).

*Development of the carpophores:* Slightly metavelangiocarpous in *T. rutilans*;

slightly paravelangiocarpous in *T. platyphylla*; unknown or incompletely known in other species.

**Area:** Probably nearly cosmopolitan (in wooded regions).

**Limits:** The conspicuous cheilocystidia distinguish this genus from other *Clitocybinae*. Some authors agree with Kotlaba & Pouzar who separate from *Tricholomopsis* one species: *T. platyphylla* transferring it to a special genus - *Megacollybia*. Neither Smith who monographed *Tricholomopsis*, nor Bigelow seem to agree with this proposal nor does Kühner who transfers *Megacollybia* as a subgenus to the genus *Hydropus*. A careful comparison of *T. platyphylla* with other *Tricholomopsis* species does not reveal any differences of more than specific weight. The epicutis of the former is by no means hymeniform nor comparable with that of *Oudemansiella*, but the filamentous hyphae end up in locally often rather dense, dermatocystidioid, swollen, terminal cells. The same can be seen in species with yellow pigments like *T. elegans* Dennis and such with livid purple pileus scales like *T. araucariae* Sing. The pigment is vacuolar in both *T. rutilans* and *T. platyphylla*\*. Phylogenetically speaking, Kühner's view is probably correct insofar as it is perfectly defendable to consider *Tricholomopsis* as relatively primitive and derive *Hydropus* from both *Tricholomopsis* and *Clitocybula*. The classification of the Tricholomataceae can, however, not express such evolutionary lines and must, in a linear system, express the stages of evolution as soon as these have developed. In the recent mycoflora, descendant series of genera are nevertheless often separated by clear and sizable hiatus. By the same way of thinking I find it impossible to link *Hydnangium* and *Laccaria* into the same family even though one is derived from the other.

**State of knowledge:** 18 species are known at present to belong in the genus *Tricholomopsis* but some of them have sometimes been considered as varieties of other species of the same genus.

**Practical importance:** *Tricholomopsis* appears to be a source of bacteriostatic substances, as promising as *Lepista*. None of the species of *Tricholomopsis* is a first class edible mushroom although most of them have been registered as edible, but according to Goos & Shoop (*Mycologia* 72: 433. 1980) and Goos (76: 350-1. 1984) *T. platyphylla* has caused poisoning in America.

## SPECIES

Sect. 1. *TRICHOLOMOPSIS* (*Rutilantes* Sing. 1943). Pileus with deep carmine, light red, yellow, olive, violet-livid, fulvous rusty brown, or blackish fuscous fibrils, or scales; lamellae yellow, livid or cream-white.

**Type species:** *T. rutilans* (Schaeff. ex Fr.) Sing.

*T. rutilans* (Schaeff. ex Fr.) Sing. (*Tricholoma*, Kummer); *T. variegata* (Fr.) Sing.

\*The discovery of further species of the *Platypyllae* in Brazil with a hyphal structure and epicutis quite different from *Hydropus* e.gr. *T. tricholomatoides* Sing. ined., confirm the position of the whole group within *Tricholomopsis*.

(if not too close to *T. rutilans*); *T. sasae* Hongo; *T. elegans* Dennis and var. *minor* Sing.; *T. decora* (Fr.) Sing.; *T. sulphureoides* (Peck) Sing.; *T. ornata* (Fr.) Sing.; *T. sulphurea* (Peck) Bigelow; *T. fimbriatophylla* (Kauffm.) Sing.; *T. flavissima* (A.H. Smith) Sing.; *T. flavescens* (Peck) Sing.; *T. subdecorosa* (Murr.) A.H. Smith; *T. araucariae* Sing.; *T. formosa* (Murr.) Sing.; *T. totilivida* (Murr.) Sing.; apparently also *T. bella* A.H. Smith; *T. ornaticeps* (Stevenson) Horak, *T. tropica* Dennis; *T. flammula* Métrod; *T. sanguinea* Hongo; *T. crocobapha* (Berk. & Br.) Pegler.

Sect. 2. *PLATYPHYLLAE* Sing. (1943). Pileus dirty dull colored; lamellae white.

Type species: *T. platyphylla* (Pers. ex Fr.) Sing.

*T. platyphylla* (Pers. ex Fr.) Sing. [Collybia, Kummer; Agaricus crassipes Schaeff.; Collybia grammocephala (Bull. ex Quél.); *T. radicata* (Peck.) Sing. (Tricholoma, Peck); *T. secedifolia* (Murr.) Sing. (Melanoleuca, Murr.); *T. tricholomatoides* Sing. ined.; *T. elatipes* Sing. ined.; apparently also *T. atrogrisea* Pegler.

Subtribus *Tricholomatinae*. Tricholomatoid; often without clamp connections and obligatorily ectomycorrhizal; spores smooth: Type genus: *Tricholoma* (Fr.) Quél.

## 27. TRICHOLOMA (Fr.) "Staude", Quél.\*

*Champ. Jura Vosges*, p. 76. 1872-73, non Benth. (1820); nom. conservandum with:

Type species: *Tricholoma flavovirens* (A. & S. ex Fr.) Lundell.

Syn.: *Tricholoma* Kummer, *Führ. Pilzk.* p. 25. 1871.

*Cortinellus* Roze, *Bull. Soc. Bot. Fr.* 23: 51. 1876.

*Gyrophila* Quél., *Enchir.*, p. 9. 1886.

*Mastoleucomyces* Batt. ex Kunze, *Rev. Gen. Pl.* 2: 860. 1891 (not validly published).

*Glutinaster* Earle, *Bull. New. York Bot. Gard.* 5: 433. 1909.

*Monomyces* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 442. 1909.

*Sphaerocephalus* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 447. 1909.

*Tricholosporum* Guzmán, *Bol. Soc. Mex. Myc.* 9: 61. 1975.

Characters: Habit of the carpophores tricholomatoid; pileus viscid, or non-viscid, glabrous or innately to tomentosely fibrillose, naked to squamose or even squarrose, rarely hygrophanous, with the pigment - where present - incrusting the hyphal walls in most of the clampless species, otherwise all dissolved in the cell-sap; cuticle consisting of interwoven, little differentiated hyphae, or of rather subparallel, thin hyphae, or of strictly parallel broad hyphae (and then hyphae most frequently without clamp connections); lamellae usually very distinctly emarginate sinuate, always strongly so in the clamp-bearing species, sometimes more adnexed or almost adnate in the clampless species, never decurrent, thin to medium thick (in some clampless species), subhorizontal, rarely subascendant at first; spore print pure white, rarely pale cream color, never truly cream-pink or pink, never greenish; spores hyaline, usually with very thin, smooth wall, inamyloid, very rarely

\*Now changed and given as "Tricholoma (E.M. Fries) Staude... T.: *Tricholoma flavovirens* (Albertini et Schweinitz: E.M. Fries) Lundell..." (ICBN 1983, p. 299). The quotation of the Code is binding as far as the definition of the taxon is concerned. The quotation should however be changed in future editions according to Art. 34.1; 34.4).

a few old spores somewhat pseudoamyloid, acyanophilic or weakly cyanophilic, ellipsoid to subglobose, more rarely fusoid, cross-shaped, or subangular, with or without suprahilar depression or appplanation; basidia normal in all regards, 4-spored, very rarely 2-spored; cystidia usually none, rarely present in the form of cheilocystidia, more rarely some cystidia present on the sides of the lamellae but then never of the *Inocybe*- or the *Melanoleuca*-type, all kinds of cystidia constantly absent in the species provided with interwoven epicuticular hyphae; hymenophoral trama regular to almost subregular, with thin parallel to somewhat interwoven rather thin, elongated hyphae; stipe central, fleshy to fleshy-fibrillose, sometimes very hard but never cartilaginous or leathery or horny in any species known, solid, stuffed, or hollow, never tubulose, veil absent, or somewhat cortina-like, or consisting of a fleshy annulus, or an annular zone at the apex of the stipe, more rarely membranous; context of the pileus fleshy, mild, acrid, or bitter, often strongly reacting with one or several of the usual reagents (formalin, phenol, KOH, methylparamidophenol, acids, etc.); hyphae ordinarily thin-walled, elongated, inamyloid, with or without clamp connections (rarely clamps absent except between the subhymenial hyphae and the basidium). Mostly on earth in the woods, more rarely in open fields, or prairies and semideserts, very rarely on wood or in deep moss (and then hyphae without clamp connections).

*Development of the carpophores:* Frequently monovelangiocarpic (about seven species of several sections of subgenus *Tricholoma* studied thus far) but in some species apparently paravelangiocarpic (e.gr. *T. focale* and *T. sciodes*). Mostly stipitocarpic but *T. focale* rather isocarpic.

*Area:* Mostly in the cold temperate to subtropical zones, very few species reaching the tropics.

*Limits:* The clampless species can be distinguished from the other fleshy genera of the *Clitocybeae* by the lack of clamp-connections and the attachment of the lamellae, the latter character distinguishing the Tricholomas from *Armillariella* and *Clitocybe*. The latter are apparently never monovelangiocarpic.

The delimitation of the clamp-bearing groups is somewhat more difficult. We consider as Tricholomas only those clamp-bearing *Tricholomataceae* which have distinctly emarginate-sinuate lamellae, white or very pale cream spore print, smooth thin-walled spores, habitat on the soil, no hirsute margin, no cheilocystidia and no pleurocystidia. In this manner, it is not difficult to eliminate such species of *Collybia* as *C. maculata* and allied forms as well as the species of *Tricholomopsis*, *Lepista*, *Hypsizygus*, *Laccaria*, etc. In fact, all the species that make it impossible to use the old Friesian delimitation between *Clitocybe* and *Tricholoma* can easily be eliminated since they form natural groups outside *Tricholoma* as well as *Clitocybe*, and the two genera, *Clitocybe* and *Tricholoma*, in the narrowest sense appear to be well distinguishable on the basis of the Friesian diagnostic characters.

There is no doubt that the genus *Tricholoma* as accepted here (and also by all other authors at present) combines a wide variety of forms ranging from species which are anatomically almost identical with *Clitocybe*, to species differing from the latter genus in almost all important anatomical characters. It is certainly tempting for

those mycologists' who give more emphasis to microscopical characters than to the external appearance, to attempt a separation of the clamp-bearing group of *Tricholoma* from the clampless group, or of the species with intracellular pigment from those with intercellular or intraparietal pigment. The species with clamp connections or with intracellular pigment would then appear to be very close to *Clitocybe* sect. 1 and the rest would be a genus *Tricholoma sensu strictissimo*. However, the author believes that this solution is not preferable since there is not a sharp line dividing the clampless from the clamped species, and the structure of the epicutis is not always correlated with the presence or absence of clamp connections or with the localization of the pigment. In addition to this it must be noted that an analysis of the available data on chemotaxonomy of *Tricholoma*\* provide a new argument in favor of the classification proposed by me since 1936. *Lepista* and *Tricholomopsis* show a different pattern of chemical substances checked thus far when compared with any of the subgenera of *Tricholoma* including subgenus *Contextocutis*. The relatively rather homogeneous chemical characters of both *Clitocybe* and *Tricholoma* would not be maintained if *Tricholoma* were to be dismembered.

*Leucocortinarius*, in spite of the pale spore print, agrees better with *Cortinarius* in all other characters, especially the margined bulb and the strongly cyanophilic episporium - and the spore print color (= Ib of Romagnesi's chart) is deeper than in any of the clamp-bearing Tricholomas.

*Armillaria* differs from *Tricholoma* in the amyloid spores, and so do all the tricholomatoid forms referable to the Leucopaxilleae. *Dermoloma* contains a few species with inamyloid spores but can be readily distinguished by the different structure of the epicutis.

Some of the species of *Lyophyllum* and *Calocybe* are externally very similar to *Tricholoma*, but differ constantly and sharply in the presence of a siderophilous granulation in the basidia. It also appears now that all species of *Tricholoma* have EM smooth spores and nodulose hilum.

There are no metuloids known to occur in any species of *Tricholoma*. This makes it easy to distinguish such white-spored Inocybes as may look like *Tricholoma* in North America.

There is no doubt but that *Lepista* and the subgenus *Contextocutis* of *Tricholoma* are closely related with each other and with *Clitocybe* but the separation on the basis of spore color and spore ornamentation still holds. The hiatus between the three groups involved is distinct enough as long as it is based on this double character (see also under *Clitocybe*). However, Bigelow has transferred *T. glaucoalbum* to *Clitocybe* on the basis of its close relationship with *Clitocybe aeruginosa*. I agree with this transfer. It becomes necessary, therefore, to exclude from *Tricholoma* sect. *Contextocutis* those species which by its color (glaucous pigments) and larger spores ( $6-8.5 \times 3.5-5 \mu\text{m}$ ) or close to crowded lamellae, lack of reddening etc. differ sharply from the rest of the species of that section. A similar precaution may be

\*For details compare Benedict, R.G., V.E. Tyler Jr., L.R. Brady and D.E. Stuntz in *Planta Medica* 12(1): 100-106. 1964.

advisable in the case of tricholomatoid specimens referable to subsection *Inornatae* of *Clitocybe* sect. *Disciformes*. Species with subfusoid-subcylindrical, elongated spores are likely to belong to *Clitocybe*.

The genus *Hebelomina* may be looked for in *Tricholoma*, but its cheilocystidia, pseudoamyloid spores with more complex thickish wall exclude it from the genus *Tricholoma*, and the Tricholomataceae in general.

**State of knowledge:** The European species of the genus *Tricholoma* were once considered as the best known group of agarics. In spite of a large amount of taxonomic work devoted to the genus *Tricholoma* since the days this opinion was published, it cannot be said that it still holds true. Several groups of species are extremely difficult and in need of monographic treatment, e.gr. *T. terreum* and allied species, *T. flavovirens* and allied species, *T. imbricatum* and allied species, *T. pessundatum* and allied species, *T. atrosquamosum* and allied species. The more extensive use of chemical reactions will probably help in segregating larger groups within the present sections. The insertion of the American, South African, Australian, and other non-European species in the scheme of subdivisions is far from complete. It would be desirable to extend the type studies on American material at least so far as to obtain the necessary microscopical data on all of them in order to be able to dispose of them in the natural classification of the genus *Tricholoma*. The classification itself appears to be sound since none of the numerous type studies on American material has essentially altered the principles on which it was founded. But the number of species that at present can be inserted is very small when compared with the number of species described. The author admits 88 species in *Tricholoma*, but the number that will appear in a future monograph will presumably be much higher.

**Practical importance:** Some species are important edible mushrooms: *T. flavovirens*, *T. albobrunneum* (which is eaten, as *T. salero*, in the Provence in salted form), *T. portentosum*, *T. mongolicum*, *T. matsutake* in Asia, and *T. ponderosum* and *T. murrillianum* in North America. *T. matsutake* is economically the most important and the most delicious species of all. It is collected in enormous quantities in Japan, and sold in the markets in fresh as well as in frozen and dried condition and in cans. It is also claimed that it has anti-tumor activity. But for every good edible *Tricholoma*, there is a poisonous one (e.gr. *T. stans*, *T. pardinum*, *T. atrosquamosum*, and perhaps forms of the *sulphureum*- and the *virgatum*-group, possibly also *T. aff. flavobrunneum* and *T. aff. sejunctum* according to Pilát (1951). *T. sulphureum* contains muscarine and epimuscarine (Stadelmann et al., Helv. Chim. Acta 59: 2434. 1976). Anybody who wants to exploit the edible species in this genus has to become an expert in distinguishing them from the non-edible species and those with unknown qualities. Among the potentially important species, one may name all the mycorrhizal species and a number of species (such as *T. saponaceum*) that have been shown to have antibiotic properties. Among the former (mycorrhizal) species, some are specific for conifers, or for *Pinus* in particular (*T. flavovirens*, *T. pessundatum*, *T. matsutake*, *T. flavobrunneum*, etc.), or for *Larix* in particular (*T. psammopodium*), and some are specific for frondose trees, many

species for *Nothofagus* in particular. A few species do not seem to form mycorrhiza at all, especially some species in the subgenus *Contextocutis*, particularly all *Leucorigida*.

## SPECIES

**Subgenus I. *Contextocutis* Sing. (1945) (= sect. *Contextocutis* Sing. 1943, p.p.).** All hyphae with clamp connections; cuticle of strongly and thoroughly interwoven hyphae, little differentiated (denser); pigment exclusively intracellular or absent; mycelium forming mycorrhiza or developing independent of mycorrhiza.

*Type species:* *T. saponaceum* (Fr.) Kummer.

Sect. 1. **LEUCORIGIDA** Sing. (1945). Pileus, lamellae, and stipe pale fuscidulous or buff to white; spores ellipsoid; mycelium growing independent of forest trees, often in fields, meadows, prairies, steppes, semideserts, etc.

*Type species:* *T. mongolicum* Imai.

*T. mongolicum* Imai; *T. altaicum* Sing.; *T. farinaceum* (Murr.) Murr.; *T. praegrande* (Berk.) Sacc. (*T. giganteum* Mass.); *T. cystidiosum* Cifuentes & Guzmán (*T. giganteum* ss. Hongo non Mass.); perhaps also *T. pratense* Pegler & Rayner, and *T. lobayensis* Heim.

Sect. 2. **RIGIDA** (Fr. em.) Sing. (1945). Pigmented species, sometimes characteristically discoloring with strong acids; spores ellipsoid, or almost subglobose, or fusoid, pure white in print; mycelium sometimes growing independently of forest trees (?) but mostly forming some kind of mycorrhiza, or at least having some symbiotic or epibiotic relation with trees. - At least *T. sudum* is very closely related to *Clitocybe*, section *Disciformes*.

*Type species:* *T. saponaceum* (Fr.) Kummer.

*T. boreale* (Fr.) Karst.; *T. sudum* (Fr.) Quél. sensu Lange non Josserand [? = *T. subluridum* (Murr.) Murr. = *T. watsonii* (Murr.) Murr.]; *T. saponaceum* (Fr.) Kummer [? = *T. oliveum* Burt; ? = *T. ferruginascens* (Murr.) Murr.]; *T. viriditinctum* (Peck) Sacc.; *T. huronense* A.H. Smith. - Also a species similar to *L. irina* with smooth, white spores (possibly = *Lepista singeri* Harmaja) and *T. singeri* Kuthan non Kühn.

Sect. 3. **IORIZIDA** Sing. (1945). Pileus, stipe, or lamellae, or all of them, with a purplish, or violet, or lilac-vinaceous tint; spores pure white or pale cream color (not pink) in print, with very thin walls, cross-shaped or subangular. Biologically similar to the species of sect. 1 or 2.

*Type species:* *T. pseudosordidum* Sing.

*T. pseudosordidum* Sing.; *T. goniospermum* Bres.; *T. porphyrophyllum* Imai; apparently also *Tricholosporum subporphyrophyllum* Guzmán and *Gymnopus atroviolaceus* Murr.

Subgenus II. *Sericicutis* Sing. 1951 [= sect. *Sericella* (Fr.) Quél. ss. lato]. Hyphae either all without clamp connections, or some clamps present either on the base of the basidia, or scattered in the carpophore or in the covering of the stipe; if clamps are found on the hyphae of the apex of the stipe, the carpophores are little pigmented (yet growing in the woods, and pileus not viscid) and have a strong characteristic odor of the flowers of *Philadelphus* or *Inocybe corydalina*, or of hemp, or of lighting gas; cuticle consisting of interwoven to subinterwoven-subparallel hyphae (occasional strands of parallel hyphae); pileus, at least its marginal portion, consequently macroscopically sericeous; mycelium of some species known to form ectomycorrhiza.

Type species: *T. sulphureum* (Bull. ex Fr.) Kummer.

Sect. 4. *SERICELLA* (Fr.) Quél.; *Sulphurea* Konr. & Maubl. Clamp connnections sometimes present; odor striking; lamellae close to distant. Type species. as in the subgenus.

*T. album* (Schaeff. ex Fr.) Kummer; *T. sulphurescens* Bres.; *T. stiparophyllum* Lund; *T. lascivum* (Fr.) Gillet sensu Lange; *T. inamoenum* (Fr. ex Fr.) Quél.; *T. platiphyllum* (Murr.) Murr.; *T. sulphureum* (Bull. ex Fr.) Kummer; *T. chrysenteroides* (Peck) Sacc. [*T. malodorum* (Murr.) Murr.]; *T. bufonium* (Pers. ex Fr.) Gillet; *T. sulphurellum* Rick; *T. odorum* Peck; *T. rhodophyllum* (Métrod) Sing.

Sect. 5. *POLYPHYLLINA* Sing. (1943, ut subsectio). Clamp connections constantly absent except at the base of the basidia; lamellae close to crowded; pileus mostly pigmentless or almost so, not viscid. Odor and taste often farinaceous; hyphae of epicutis 2-5(7)  $\mu\text{m}$  broad.

Type species: *T. columbetta* (Fr.) Kummer.

*T. columbetta* (Fr.) Kummer; *T. virginicum* (Murr.) Murr.

Subgenus III. *Pardinicutis* Sing. (1961). Clamp connections present; cuticle of pileus consisting of not interwoven, but rather subparallel hyphae which make the pileus superficially tomentose and more or less squamose, not viscid; odor weak or none; spores relatively large ( $8-10 \times 5-7 \mu\text{m}$ ); pigment well developed in cuticle of pileus.

Type species: *T. pardinum* (Pers. ex) Quél. (*T. pardalotum* Herink & Kotlaba).

Sect. 6. *PARDINICUTIS*. Characters of subgenus and same type.

*T. pardinum* (Pers. ex) Quél.; probably also *T. cedrorum* Maire.

Subgenus IV. **Tricholoma** (*Eu-Tricholoma* Lange 1933; *Armillaria* subg. *Verarmillaria* Imai 1938). Clamp connections never (or very exceptionally\*) present; pigment usually intraparietal and/or distinctly incrusting the hyphal walls (if present); cuticle a cutis as in the preceding section but the parallel hyphae of which it

\*Occasional clamps are observed in the lower surface of the stipe in certain species since in these the mycelium is clamped while in others it is clampless; occasional clamps can also be found at the base of the basidia in some species (e.gr. *T. gausapatum* according to Huijsman, *Schweiz Zeitschr. f. Pilzk.* 9: 148. 1968).

consists rather broad if the pileus is dry, and narrower if the pileus is viscid, macroscopically, the pileus is hygrophanous or more frequently dry (and then cuticular hyphae 7  $\mu\text{m}$  or more in diameter), or viscid (and then hyphae usually 2-4-6  $\mu\text{m}$  in diameter), in the latter case either glabrous or not glabrous, if dry, rarely subglabrous, usually either tomentose, or tomentose-scaly, or squamulose, squamose, squarrose, rimose, fibrillose, etc., never sericeous, and rarely hirsute on the margin; odor of *Philadelphus* or gas (as described in subgenus *Sericeicutis*) absent in the species with dry cuticle; mycelium mycorrhizal in probably all species.

*Type species:* *T. flavovirens* (A. & S. ex Fr.) Lundell in Lundell & Nannfeldt.

Sect. 7. *TRICHOLOMA* [*Limacina* (Fr. ut sect. *Agarici* trib. *Tricholomatis*) Quél. (1872-73) em. Sing. (1945); *Equestria* Konr. & Maubl. (1924-37; *Terrea* Konr. & Maubl. 1924-37]. Pileus gray, umber, whitish with grayish fibrils, or golden lemon yellow (or a mixture of these colors) never hygrophanous; lamellae white, yellowish, gray, or pink, never rusty spotted.

*Type species:* As in subgenus.

Stirps *Flavovirens* (pileus viscid, fibrillose, or glabrous; lamellae mostly yellowish): *T. flavovirens* (A. & S. ex Fr.) Lundell apud Lund & Nannf.; *T. sejunctum* (Sow. ex Fr.) Quél. (with several varieties); *T. subsejunctum* Peck; *T. angustifolium* (Murr.) Murr.; *T. yatesii* (Murr.) Murr.

Stirps *Portentosum* (pileus viscid, or subviscid, innately fibrillose; lamellae mostly white): *T. portentosum* (Fr.) Quél. and var. *leucoxanthum* Gillet; probably also *T. dryophilum* (Murr.) Murr.; *T. niveipes* Peck; *T. peralbum* (Murr.) Murr.

Stirps *Virgatum* (taste acrid, spores rather broad; cheilocystidia present but sometimes sparse): *T. virgatum* (Fr. ex Fr.) Kummer; *T. subacutum* Peck; *T. sciodes* (Secr.) Martin; *T. lilacinocinereum* Métrod; *T. acre* Peck (*T. subacre* (Murr.) Murr.)

Stirps *Scalpturatum* (a cortina or a membranous veil present; generally without a distinct cellular hypodermium, at least in *T. sculpturatum* and *T. cingulatum*; spores generally smaller and more elongated than in the following stirps): *T. argyreum* (Kalchbr.) Sing.; *T. triste* (Fr.) Quél. (taken to stirps *Terreum* by Cléménçon because of the cellular-vesiculose hypodermium); *T. ramentaceum* (Bull. ex Fr.) Ricken (sensu Bres.); *T. sculpturatum* (Fr.) Quél. (sensu Bres.); *T. romagnesii* Sing. (*T. ramentaceum* sensu Romagnesi); *T. cingulatum* (Almfelt ex Fr. Jacobasch; possibly also *T. albatum* (Quél.) D'Astis & Maubl.)

Stirps *Terreum* (Not acrid, not viscid, veil cortiniform and fugacious, or absent; spores up to 8  $\mu\text{m}$  long): *T. terreum* (Schaeff. ex Fr.) Kummer; *T. myomyces* (Pers. ex Pers.) Lange; *T. gausapatum* (Fr.) Quél. sensu Bres. (an sensu Fr.?); *T. subterraneiforme* (Murr.) Murr.; *T. moseri* Sing. (spores 7.3-8.8  $\times$  3.5-4.3  $\mu\text{m}$ , possibly to the following stirps since hypodermium not containing swollen elements, but formalin reaction unknown).

Stirps *Atrosquamosum* (Positive reaction with formalin (usually reddish); stipe

often granulose; cheilocystidia usually present; poisonous): *T. atrosquamosum* (Chev.) Sacc.; *T. nigromarginatum* Bres.; *T. squarrulosum* Bres.; *T. orirubens* Quél.; perhaps also *T. luteomaculosum* A.H. Smith (unless this is a closely related stirps) and the *T. sudum* sensu Josserand (non Fr.).

Sect. 8. *GENUINA* (Fr.) Sacc. (*Citrinofulva* Sing. 1943; *Albobrunnea* Konr. & Maubl. 1924-37, Kühner, Kühner & Romagnesi). Pileus cinnamon, buff, orange, rufous-castaneous, chestnut-brown, tawny, etc. or in any of these colors mixed with pallid or white (resulting a sordid ochraceous to stramineous general effect); lamellae white, buffy pallid, light yellowish, often with rusty, rarely with blackish spots, especially in old specimens; taste more often bitter than acrid, but also often mild.

Type species: *T. vaccinum* (Pers. ex Fr.) Kummer.

Stirps *Caligatum* (annulate): *T. colossus* (Fr.) Quél.; *T. robustum* (A. & S. ex Fr.) Ricken; *T. caligatum* (Viv.) Ricken; *T. matsutake* (S. Ito & Imai) Sing. (*Armillaria*, S. Ito & Imai); *T. ponderosum* (Peck) Sing. (*Armillaria*, Peck); *T. murrillianum* Sing. (*Armillaria arenicola* Murr.); obviously also *T. focale* (Fr.) Ricken ss. Ricken; probably also *T. coarctatum* Cooke & Mass.

Stirps *Cortinatum* (strongly cortinate; pileus viscid or not; stipe generally fibrillose-rough furfuraceous or granulose; subantarctic group): *T. cortinatum* Sing.; *T. cortinatellum* Sing.

Stirps *Acerbum* (stipe furfuraceous or granulose; pileus without reddish or chestnut tinge): *T. acerbum* (Bull. ex Fr.) Quél. sensu Bres.: *T. psammopodum* (Kalchbrenner) Quél.

Stirps *Imbricatum* (Margin of pileus woolly-projecting, or with a weak cortina, but then stipe non-furfuraceous or evelate; pileus dry even in rainy weather; lamellae not yellowish when quite fresh; color some kind of reddish brown): *T. imbricatum* (Fr. ex Fr.) Kummer; *T. inodermeum* (Fr.) Gillet; *T. vaccinum* (Pers. ex Fr.) Kummer; *T. arenicola* (Murr.) Murr.

Stirps *Transmutans* (veil absolutely none; pileus viscid in very wet conditions, but fibrillose when dry or at least tomentose-rough in parts; lamellae often yellowish when young; color some kind of reddish brown): *T. subtransmutans* (Murr.) Murr.; *T. flavobrunneum* (Fr.) Kummer (*T. transmutans* (Peck) Sacc.).

Stirps *Aurantium* (Stipe "subannulate", i.e. with annular zone; context often bitter): *T. albobrunneum* (Pers. ex Fr.) Kummer (A. salero Barla) *T. aurantium* (Schaeff. ex Fr.) Ricken; *T. subannulatum* (Batsch ex) Bres. (*T. batschii* Gulden); *T. californicum* (Murr.) Murr. (unless it is too close to the preceding species).

Stirps *Pessundatum* (Pileus viscid, stipe not zonate or very indistinctly so; context usually not bitter but often poisonous; spores ellipsoid): *T. pessundatum* (Fr.) Quél.; *T. stans* (Fr.) Sacc.: *T. ustale* (Fr. ex Fr.) Kummer (f. *minor* Fr. cet. excl.); *T. populinum* Lange; *T. earleae* (Murr.) Murr.

The following species from the *Nothofagus* region are closest to the preceding stirpes but may be considered a stirps of their own:

*T. fagnani* Sing.; *T. ochraceorobustum* Horak (with var. *cautinense* Sing.); *T. elvirae* Sing.; *T. mostnyae* Sing.; *T. fusipes* Horak; *T. patagonicum* Sing.; *T. diemii* Sing.; also apparently here: *T. inocybiforme* Horak, *T. farinolens* Horak, *T. hebelomoides* Horak, and *T. andinum* Horak.

Sect. 9. *ADUSTA* Sing. (1961). Pileus glabrous, hygrophanous, gray, umber, blackish, dull brown, olive brown, etc.; habit tricholomatoid (but with small carpophores) or almost collybioid.

Type species: *Melanoleuca adusta* Murr.

*T. adustum* (Murr.) Murr.; *T. spec. aff. adustum* from Northern North America (? *Collybia atratooides* Peck); also perhaps *Collybia olivaceobrunnea* A.H. Smith & Hesler and *T. olivascens* Boud. (The latter species, being non-hygrophanous, might be better placed in subgenus *Sericeocutis*, in a special section, *Pseudocollybia* Kühn. in Kühn. & Romagnesi nom. subnud., but unknown to me; other species placed in *Pseudocollybia* by Kühner & Romagnesi clearly refer to *Callistosporium*).

Subtribus *Omphalinae* Sing. (1970). Clampless hyphae in the carpophore frequently occurring or carpophores with latex, with numerous gloeocystidia, or strictly omphalioid or collybioid, not tricholomatoid nor clitocyboid (however if hyphae without clamp connections, clitocyboid habit does occur); obligatory ectomycorrhiza never observed, but lichenization and endomycorrhiza frequent.

Type genus: *Omphalina* Quél.

## 28. ARMILLARIELLA Karst.

*Hymenomycetes Fennici. Acta flor. faun. Fenn.* 2: 4. 1881.

Type species: *A. mellea* (Vahl in Fl. Dan. ex Fr.) Karst.

Syn.: *Armillaria*\* sect. *Armillariella*, Karst. *Bidr. Känn. Finl. Nat. Folk* 32: xii. 1879.  
*Polymyces* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: (447). 1909.

**Characters:** Habit of the carpophores clitocyboid, but lamellae sometimes slightly sinuate and subdecurrent; pigment either intracellular or intraparietal or intracellular, mostly brown or melleous to umber brown, but often with yellow parts on the carpophore, or with very deep fuscous-spadiceous scales. Pileus surface fibrillose to squamulose or squarrulose (but scales or fibrils often detersile because of an underlying gelatinized hyphal layer), hygrophanous or non-hygrophanous, not glutinous, but often somewhat viscid; lamellae close to subdistant, moderately thick, adnate-subdecurrent to deeply decurrent, but often with a slight sinuation; spore print varying from pure white to light cream, reaching a deeper cream color (Romagnesi chart IIa) when dehydrated; color not in all species quite constant.

\*The reasons why we do not recognize the generic name *Armillaria* with the type species *A. mellea* for the present genus are amply discussed under *Armillaria* Kummer. p. 304

Stipe central, fibrous-fleshy in age, often with an annular veil, not cartilaginous or tubulose-fragile but often becoming hollow, with basal mycelium and/or black rhizomorphs, the latter quite generally appearing in cultures derived from trama. Hyphal system monomitic; hymenophoral trama in primordium bilateral and either remaining so in adult specimens or becoming more regular (*Clitocybe*-subtype); hyphae without clamp connections and inamyloid in the trama of pileus, stipe, hymenophoral trama; spores with thin to moderately thick wall, smooth to longitudinally ridged (Pl. 47, 3), inamyloid (rarely a few vaguely pseudoamyloid), hyaline, exceptionally a few with slightly brownish wall, the outermost wall-layer mostly very weakly cyanophilic\*, otherwise acyanophilic; basidia usually 4-, sometimes some 2-spored, often among them several sclerified basidia which are mostly fertile, 7-nucleate, with or without basal clamp; cheilocystidia present, but sometimes rather inconspicuous, or catenate-septate, septa often clamped; pleurocystidia usually absent, rarely few and inconspicuous. Epicutis (underneath the bunches of subparallel ascendant or applicate broad hyphae which form the scales) of parallel to subparallel applicate hyphae forming a cutis or ixocutis. Hyphae of the scaly top layer with occasional clamps or clampless; basal mycelium and mycelium in culture often forming mycelial basidia and/or allocysts, without clamp connections or with occasional clamped septa; mycelium often luminescent; often or always passing through a diploid phase in the life cycle. Growing on dead logs or bark, and on living wood, often parasitic or endomycorrhizal, also on tufts of *Carex* and grasses, moss-beds, rarely on earth, on orchids.

*Development of the carpophores:* Bivelangiocarpous or metavelangiocarpous in the annulate species, monovelangiocarpous and stipitocarpous in *A. tabescens* and some other evelate species.

*Area:* Almost cosmopolitan excepting Antarctica and probably Amazonia.

*Limits:* *Armillariella* has often been subordinated to *Armillaria*, or *Clitocybe*. The veil-less *Armillariellas* differ from *Clitocybe* in the absence of clamp connections and the production of black rhizomorphs, the more complex structure of the covering layers, and several other secondary characters. The veiled species differ from *Tricholoma* in the more clitocyboid habit and usually lignicolous habitat, black rhizomorphs and several other secondary characters. *Omphalina* and *Gerzonema* differ in the omphaliod habit and different pigments as well as constant absence of black rhizomorphs and veil. *Pseudoarmillariella* differs in amyloid spores.

On the other hand, some species without clamp connections and similar in habit to *Armillariella*, have in the past been included in *Armillariella*. These species include clamp-less *Hygrophoraceae* which differ in the length of the basidia and affinity with species of the hygrophoraceous genera *Camarophyllus* and *Hygrotrama*. Other species, formerly considered to be congeneric with *Armillariella* have since then

\*It is possible that the cyanophilic "layer" corresponds to the ornamentation (longitudinal ridges) visible only under the scanning microscope (cf. Pegler & Young, Pl. 4, Fig. 3, 1971) in most species, but under the light microscope in *A. camerunensis*.

been removed to *Gerronema*, *Lulesia*, and *Arthrosoporella*. They can be easily distinguished from *Armillariella* by the key characters.

It should be taken into consideration also that those genera likely to be confused with evelate *Armillariella* are, as far as we know now, all gymnocarpous. The only species obviously not gymnocarpous is *Hygrotrama hiemale* which also has the occurrence of sclerobasidia in common with *Armillariella*. Nevertheless, the pigments of *H. hiemale* are quite different and the basidia elongate as in most Hygrophoraceae.

*State of knowledge:* Only since Singer (1956, 1969, 1970, 1977) and later Romagnesi (1970, 1983) and Singer & Cléménçon (1973) have shown that several well distinguishable species make up the *A. mellea* complex, has the taxonomy of the genus become meaningful. It cannot be enough emphasized that valuable papers on development, physiology, and sexuality as well as phytopathology and phytogeography of the genus should be backed up with specific determination of the organisms involved, or at least specimens with all necessary annotations on spore print color (not dehydrated), taste, and color of the specimens be made available for later verification. At present 24 species are recognized.

*Practical importance:* Many species of the *A. mellea*-complex and *A. tabescens* are very important as wood destroyers, pathogens, symbionts (endomycorrhiza!) of heterotrophic orchids, and edible fungi with considerable commercial value. Many diseases of forest-, park- and fruit-trees as well as vegetable crops are caused by them (see also p. 224).

## SPECIES

### 1. Annulate species (The *A. mellea*-complex).

*A. mellea* (Vahl in Fl. Dan. ex Fr.) Karst. (*Agaricus ingricus* Weinmann); *A. praecox* (Velen.) Sing.; *A. polymyces* (Pers. ex S.F. Gray em. Secr.) Sing. & Cléménçon; *A. saviczii* Sing.; *A. puiggarii* (Speg.) Sing.; *A. bulbosa* (Barla) Romagnesi; *A. sparrei* Sing.; *A. melleorubens* (Berk. & Curt.) Sing.; *A. procera* (Speg.) Sing.; *A. olivacea* (Rick) Sing.; *A. obscura* (Schaeff. ex Secr.) Romagnesi (*A. montagnei* var. *umbrinobrunnea* Sing.); *A. montagnei* Sing.; *A. novaezelandiae* Stevenson; *A. limonea* Stevenson; *A. griseomellea* Sing.; *A. omnituens* (Berk.) Sing.; *A. yungensis* Sing.; *A. camerunensis* (Henn.) Sing.\*; obviously also *A. ostoyae* Romagnesi, *A. elegans* Heim, *A. fellea* Hongo; *Armillaria fuscipes* Petch *A. cepaestipes* Velen; *A. fumosa* Kile & Watling; *A. hinnulea* Kile & Watling; *A. luteobubalina* Watling & Kile in Podger et al. and possibly several others including a white species or variety (of *A. polymyces*?) kindly sent to me from Berlin by Dr. Poelt and perhaps *A. mori* (Paul. ex Fr.) Sacc.

### 2. Exannulate species:

\*c.n. (*Armillaria mellea* var. *camerunensis* Henn., Engl. Bot. Jahrb. 22: 107. 1895), with the spores longitudinally ridged under the light microscope.

*A. tabescens* (Scop. ex Fr.) Sing.; *A. ectypa* (Fr.) Sing.; *A. watsonii* (Murr.) Sing.; *A. nigropunctata* (Secr.) Sing.

## 29. ARTHROSPORELLA Sing.

*Flora Neotropica* 3: 17. 1970.

*Type species: Arthrosporella ditopa* (Sing.) Sing.

*Syn.: Nothoclavulina* Sing. l.c., p. 18 (imperfect stage).

*Characters:* Habit clitocyboid; stipe and pileus arthrospore-bearing; basidiospores ellipsoid, inamyloid; cystidia none; hyphae without clamp connections, inamyloid; hyphal structure monomitic. On rotting leaves and other débris and on humus in the forest. - Imperfect state: Habit of *Clavulina*, pulverulent from externally formed white arthrospores which are unicellular or with few septa, thin-walled, smooth. Pl. 43.

*Development of the carpophores:* Unknown but apparently gymnocarpous.

*Area:* Subtropical South America.

*Limits:* Differs from *Armillariella* in the arthrospore-bearing stipe and pileus.

*State of knowledge:* Only one species is known at present.

*Practical importance:* Unknown.

## SPECIES

*Arthrosporella ditopa* Sing. - Imperfect state: *Nothoclavulina ditopa* Sing.

## 30. LULESIA Sing.

*Flora Neotropica* 3: 16. 1970.

*Type species: L. densifolia* (Sing.) Sing.

*Characters:* Habit clitocyboid; epicutis trichodermial; spores minute, hyaline, inamyloid, smooth, but in certain media often appearing slightly rounded-angular or nodulose; cystidia none; stipe solid, without arthrospore formation; hymenophoral trama regular, hyphae without clamp connections, inamyloid. Stipe evelate; white rhizomorphs often abundant; black rhizomorphs none. Thermophilous in forests, on the ground.

*Development of the carpophores:* Unknown.

*Area:* Southern subtropical zone in the Western Hemisphere.

*Limits:* *Lulesia* differs from *Armillariella* by the combination of characters

emphasized in the keys and the generic description, particularly the absence of black rhizomorphs, the minute spores and the trichodermial epicutis. It differs from *Clitocybe* in the absence of clamp connections combined with the trichodermial epicutis.

The characteristics of this monotypic genus are only partially known since the material has not recently been restudied and no additional collections have been made. It is here assumed that the spore print is white or cream, and that the smoothness of the spore wall as seen in methylene blue, carmine-acetic acid and Melzer excludes genera with rough spores. It is not known whether the spores are cyanophilic or binucleate, and nothing is known about the topography of the pigment. The fact that *Clitocybe alachuana* Murr. which I once believed to be congeneric, actually belongs to *Rhodocybe*, brings up the question whether *Lulesia densifolia* is sufficiently different from *Rhodocybe*. If it is, it should be carefully compared with *Gerronema* sect. *Gerronema*, particularly *G. collybiomorphum*.

*State of knowledge:* Only one species known.

*Practical importance:* Unknown.

## SPECIES

*L. densifolia* (Sing.) Sing.

### 31. ARRHENIA Fr.

*Summa Veg. Sc.* 2: 312. 1849.

*Type species:* *Arrhenia auriscalpium* (Fr.) Fr.

*Characters:* Carpophores at first pezizoid-stipitate, with a central or eccentric apical opening, later spoon-shaped to spatuliform and bending over so that the hymenium becomes directed towards the ground (nutant); pseudostipe eventually longer than pileus diameter; hymenophore consisting of veins which are often meruloid-anastomosing in mature specimens, separated from the stipe by a sterile rim in continuation of the pileus-margin; basidia chiastic, with 4 sterigmata; spores in print probably white or whitish, hyaline under the microscope, smooth, inamyloid, medium sized (up to 10 µm), short ellipsoid to ellipsoid or guttiform; cystidia none. Trama consisting of filamentous, non-gelatinized hyphae with membranal incrusting fuscous pigment, with clamp connections, inamyloid. Sterile surfaces of applicate or irregularly protracted but little differentiated hyphal ends which may be occasionally forked or uneven. On earth among mosses, lichens, and herbs, often overgrowing living mosses and herbs but not exclusively bryogenous and apparently not parasitic.

*Development of the carpophores:* According to Pilát the youngest carpophores seen were cup-shaped (with an ellipsoid upper portion) in the hollow inner portion of

which the hymenium begins to differentiate, directed away from the substratum later becoming spatulate and nutant, the hymenial surface turning more towards the substratum and becoming gradually ornamented, from the beginning with a (pseudo-)stipe and with an apical narrow opening, thus apparently gymnocarpous.

*Area:* In the temperate to frigid regions, Alps, Northern Europe, and Western North America.

*Limits:* This differs from the comparable genera in its shape and the development of the carpophores from pezizoid to nutant, the configuration of the hymenophore, and the absence of cystidia. It comes undoubtedly closest to *Leptoglossum* from which it may be distinguished by the habit, eventually nutant stipe and perhaps the habitat. The spore print has been indicated as reddish by various European authors but in the species here considered as the true *A. auriscalpium* (sensu Favre, Pilát) it is whitish. If then the spore print is actually not distinctly colored in the European species, the distinction from certain species of *Leptoglossum* is exclusively based on the shape of the fruiting bodies. Kühner (1980) and Moser (1978, 1983) think that *Arrhenia* is congeneric with *Leptoglossum*, a position that depends on one's concept of the genus in this group (Omphalinae).

Therefore, it would follow that in spite of the surprising similarity in the habit of the carpophores and the configuration of the hymenophore, *Merulius pezizoideus* Speg. is not, as Patouillard thought, congeneric with *Arrhenia auriscalpium*, at least in the sense of Pilát and Favre. It may, however, still be congeneric with that conception of *Arrhenia auriscalpium* which is indicated as having red spores. If it is, both the latter and *Merulius pezizoideus* have nothing to do with *Arrhenia* as accepted here. They are better placed in the Meruliaceae or some other subdivision of the Aphyllonales than in the Tricholomataceae (cf. *Rhodoarrhenia*, p. 852).

*State of knowledge:* Only the type species has been studied thoroughly. Other species of *Arrhenia* found in the literature are still rather doubtful or should be excluded, especially *A. fimicola* whose type (G) is a Discomycete.

*Practical importance:* Unknown.

## SPECIES

*A. auriscalpium* (Fr.) Fr. (*Cantharellus*, Fr.; *Cantharellus muehlenbeckii* Trog.).

## 32. LEPTOGLOSSUM Karst.

*Bidr. Finl. Nat. Fölk* 32: xvii, 242. 1879 non (Cooke) Sacc. (1884).

*Type species:* *Cantharellus muscigenus* (Bull. ex) Fr.

*Syn.:* *Leptotus* Karst., l.c.

*Corniola* S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 637. 1821 non Adams. (1763).

*Dictyolus* Quél., *Enchir. F.* p. 139. 1886.

*Geotus* Pilát, *Ceská Mykologie* 7: 9. 1953.

*Phaeotellus* Kühn. & Lamoure, *Le Botaniste* 55: 24. 1972.

**Characters:** Habit omphalioid, pleurotoid or pezizoid with pseudostipe or without one; small to medium sized, soft to soft-cartilaginous, hymenophore lamellate (lamellae very narrow and often crisp or anastomosing or with reniform lamellulae, often not reaching the margin) and then stipe mostly lateral, eccentric or absent, or hymenophore consisting of veins, hymenial surface never quite smooth in mature specimens, covering the portion directed towards the substratum or earth. Trama not gelatinized, consisting, seemingly or actually, of a single kind of filamentous hyphae, strictly monomitic, with or without clamp connections, inamyloid. Pigment always present and typically incrusting or membranal, fuscous or fuliginous or ocker-brownish. Spores cylindric-oblong, ellipsoid, or short-ellipsoid, not globose or fusoid, smooth, thin-walled, inamyloid. Spore print white. Cuticular layer not much differentiated, hyphous, of appressed elements. Cystidia or cheilocystidia none. Typically on living mosses, but also (rarely) on earth among mosses or on mossy logs.

**Development of the carpophores:** Gymnocarpous.

**Area:** Mainly temperate and frigid zones of the Northern and Southern hemispheres.

**Limits:** This genus was originally thought to contain only the stipitate species with pleurotoid habit and cantharelloid (veins) hymenophore. Persoon combined it with *Merulius*, Fries with *Cantharellus*. Karsten put the astipitate species in a special genus, *Leptotus*. This latter genus was originally (1945, 1951) accepted by the present author to include all species, but as was pointed out by various other authors, Ricken (1910) had previously to this used *Leptoglossum* in a broad sense. Omphalioid species entered the group only when it was emended by Singer (1951) to accommodate *Pleurotus tremulus* which differs from the rest of the species only in habit. It was left out of the Agaricales proper by many modern authors because of its reduced form and structure, but a broader view at the problem became possible when it was shown (Singer 1945) that other genera of the "Leptotaceae" had actually close affinities with either the agarics proper or groups of the Aphyllophorales, particularly when it became necessary to introduce *Campanella* in the Tricholomataceae because of its close affinity with the Resupinateae and Collybieae.

As for *Leptoglossum* and *Arrhenia*, they have an impressive number of characters in common with *Omphalina*, and far from belonging in a separate family ("Leptotaceae" or "cantharelloid fungi") their delimitation from *Omphalina* is often difficult even if the typical carpophores of both genera differ widely from typical *Omphalinas*. All species with veins instead of lamellae (including species with narrow, crisp, often anastomosing lamellae) belong in *Leptoglossum* or *Arrhenia*, not in *Omphalina*. Likewise all species with eccentric, or lateral (or wanting) stipe belong not in *Omphalina* but in *Leptoglossum*.

Kühner (1980) prefers to combine *Phaeotellus* where the hymenophore is more

lamellate and the stipe in the primordium central, with *Arrhenia* where he also includes *Leptoglossum* (and *Leptotus*). If such a wider generic concept is adopted, it would have been preferable, in my opinion, to also include *Omphalina* because the position of *Omphalina* (or, according to Kühner, *Phaeotellus*) *griseopallida* is ambiguous even in Kühner's scheme. It must be admitted that the delimitation of *Leptoglossum* in our sense from *Omphalina* is still difficult. Both genera would perhaps be better circumscribed if *Phaeotellus* were recognized as a separate unit, but, considering the world flora, the separation of *Phaeotellus* from *Omphalina* and *Leptoglossum* sensu stricto is still very difficult inasmuch as the group of *L. acerosus* and *L. tremulus* is not sufficiently explored. Neither the predominant number of nuclei in the spores nor the pigment topography provides a generic character in this case and the presence or absence of clamp connections is variable in *Leptoglossum* as well as in *Omphalina*. What remains is the macroscopical characters of the hymenophore and the attachment of the stipe (as well as its development from the primordium to the mature carpophore), and the habitat (on living mosses, on wood, or earth).

Another problem has arisen with regard to the non-pigmented species referred by some authors to *Leptoglossum*. Corner (1966) in particular and, following him, Agerer (1984) consider *Mniopetalum* congeneric with *Leptoglossum*, an opinion I do not share for reasons given by me (1970, p. 78). *Leptoglossum*, as *Omphalina*, is by definition provided with a pigment which is typically quite distinctly intraparietal and ± incrusting. Redhead, although with a somewhat wider genus concept (1984) came to the same conclusion.

*State of knowledge:* Some groups of species in this genus are still in need of further studies, but several species are completely known; 9 of these have been inserted here.

*Practical importance:* Unknown.

## SPECIES

**Subgenus Phaeotellus** (Kühn. & Lamoure) Sing. stat. nov. (*Phaeotellus* Kühn. & Lamoure, l.c.; *Arrhenia* subgen. *Phaeotellus* (Kühn. & Lam.) Kühn. 1980). Stipe well developed, eventually ± eccentric to lateral; lamellae well developed, at least partially (even though often forked and/or anastomosing or not reaching the margin). Mostly not directly on living mosses but on earth among mosses, on bare earth or sand or gravel, or on wood.

*Type species:* *A. acerosus* Fr.

Species with clamp connections:

*L. acerosum* (Fr.) Moser and related forms and species; *L. tremulum* (Schaeff. ex Fr.) Sing.; *L. andinum* Corner; *L. alnetorum* Sing. (*Arrhenia*, Redhead as *A. "alnetora"*).

Species without clamp connections:

*L. rickenii* (Sing. ex Hora) Sing. c.n. (*Omphalina rickenii* Hora, *Trans. Brit. Myc. Soc.* 43: 454. 1960).

Subgenus **Leptoglossum**. Stipe poorly developed or lateral from the beginning (primordia), sometimes none, or replaced by a pseudostipe; lamellae at first none, soon with a venose (often anastomosing in part) hymenophore; carpophores sometimes multipileate. Mostly growing on living mosses.

Type species: *Cantharellus muscigenus* (Bull. ex) Fr.

Species with clamp connections:

*L. retirugum* (Bull. ex Fr.) Karst. sensu Kühn. & Romagnesi; Sing. *L. lobatum* (Pers. ex Fr.) Ricken; *L. uliginosum* (Pers.) Sing. (unless too close to the preceding species).

Species without clamp connections:

*L. muscigenum* (Bull. ex Fr.) Karst.; *L. conchatum* Velen. non sensu Kühn. & Romagnesi (*L. retirugum* sensu Redhead); apparently also *Phaeocyphella muscicola* (Fr.) Rea sensu Bourdot 1932.

### 33. OMPHALINA Quél.

*Enchiridion Fung.* p. 42. 1886.\*

Type species: *O. umbellifera* (L. ex Fr.) Quél. sensu Quél. (= *O. pseudoandrosacea* (Bull. ex St-Amans) Moser. - An alternative choice made by Redhead & Weresub, Cléménçon, and Kühner: *O. epichysium* (Pers. ex Fr.) Quél.\*\*

\**Omphalina* Quél. is certainly not an avowed substitute for *Omphalia* thus not a nomen novum, and consequently, according to the provisions of the Code Art. 7 and 31, to be typified independently of the type species of *Omphalia*, as had already correctly been stated by Rogers (*Farlowia* 4: 29. 1950). Not only is an indication that *Omphalina* is a nomen novum absent from Quélét's writings but he accepts since 1886 *Omphalina*. Quél. as a split group from *Omphalia* Persoon, part of which is maintained as such, and part of it (some species of sections *Minores* Pers., *Synopsis* p. 466) enters the new genus *Omphalina*. Interpreting Quélét's new (1888) classification, Magnin, L. & A. Chomette (*Suppl. Bull. Soc. Myc. Fr.* p. 66, 1909), treat *Omphalina* as "genre nouveau, voir Quélét ..." *Omphalia* was 1886 erroneously called *Omphalia* Quél., (instead of (Pers.) Quél.); only 1888 it reads *Omphalia* Pers. Certainly, Gray was the first to use *Omphalia* on the generic level referring to a pre-starting-point work (Persoon, as a section) and therefore it is his protologue that determines the type (according to Art. 7.12). None of Gray's species is an *Omphalina*. The first selection of a type of *Omphalia* was Singer & Smith: *O. adusta*. Thus, even if *Omphalina* were a new name for *Omphalia* sensu Quél., (Fr.) Quél. or whatever, if would still have to have a different type from *Omphalia* (Pers. ex) Gray. It is my opinion that Gray effectively restricted and emended Persoon's conception and that later authors referring to *Omphalia* (Pers.) Quél. either misapplied the name or created a (superfluous) homonym. As for *Omphalia* (Fr.) Quél. (referred to by Quélét as *Omphalia* Quélét, and *Omphalina* Quél.) we refer to foot note \*\*.

\*\*Singer & Cléménçon (1973) have shown that *Omphalina umbellifera* as understood by Quélét 1886 is a species of the dark gray group with incrusting and intraparietal pigment, and that, obviously, the type species of Quélét's genus must be interpreted in the sense of Quélét which is not the sense of (L. ex Fr.) M. Lange (this latter species belongs in *Gerronema*!). The reference, by Quélét, to Bulliard's plate 276 (*A. pseudoandrosaceus* Bull.) which shows a fuscous fungus, "albicans" as Quélét says i.e. hygro-

*Syn.*: *Omphalia* (Fr., tribus 1821) Quél., *Champ. Jura Vosg.* p. 101, 1872-73, non (Pers. ex) Gray neque *Omphalea* L. (1759). Type: *A. epichysium* Pers. ex Fr.  
*Omphalia* Kummer, *Führ. Pilzk.* p. 28. 1871 non *Omphalia* (Pers. ex) Gray neque *Omphalea* L. (1759). Type: *O. epichysium* (Pers. ex Fr.) Kummer  
*Phalomea* NieuL., *Am. Midl. Nat.* 4: 381. 1916.

**Characters:** Habit of the carpophores distinctly and constantly omphaliod; pigment generally present, often abundant, intraparietal and mostly incrusting, never carotinoid or xanthinic, either dull colored (gray to almost black) or bright colored (brown, green, purple, etc.); pileus more or less hygrophanous, glabrous and naked or with scales near the center, with straight or incurved margin, often umbilicate; cuticle consisting of radially arranged, filamentous hyphae and generally little differentiated; lamellae decurrent, sometimes comparatively thick and distant and thus reminding one of *Camarophyllus* or *Hygrocybe* of the Hygrophoraceae; spore print pure white or rarely pink; spores hyaline, smooth, with thin, or rather thin, inamyloid and homogeneous walls, short-ellipsoid, ellipsoid, ovoid, very broadly cylindric, oblong, or tilda-shaped; basidia normal in all regards, but frequently 2-

phanous. Bulliard adds that "it is sometimes of a yellowish white" which refers to an atypical form which we now know is *G. ericetorum*, and which Quélet, along with his generation, considered to be a variety of *O. umbellifera*. A confirmation of this interpretation is found in *Flore Mycologique* (1888) where the type variety is described as "gris, bistré, paille, blanchâtre ou ocracé, blanchissant", i.e. in the first place of the color range indicated in Bulliard's plate. Quélet (1895) expressly interprets Bulliard's *A. pseudoandrosaceus* Pl. 276 as his *O. umbellifera*. The identity of the type form of *O. umbellifera* is not difficult to establish. The white or cream lamellae fit only young carpophores of *O. grisella* (Weinm.) Moser in Gams. The confusion about *O. umbellifera* and *O. ericetorum* goes back to Fries, *Syst. Mycol.* 1: 165. 1821, where *A. ericetorum* is based not on Persoon (whose *A. ericetorum* is gray!) but on Fries, *Observ.* 1: 87. 1815-18 which is *G. ericetorum* (Fr. ex Fr.) Sing. for which Fries since *Suppl. Syst. Mycol.* 1: 22. 1830 took up the name *A. umbelliferus* Linn. Quélet, on the other hand, took up Persoon's *A. ericetorum* in Persoon's sense attaching it as a synonym to *O. rustica* and distinguished *O. umbellifera* by the color of the lamellae. Fries distinguished already in 1821 a var. *grisellus* of *A. ericetorum*, quoting (erroneously) "A. S. p. 225" which is *G. ericetorum* (Fr. ex Fr.) Sing. but his other synonyms refer plainly to Quélet's type variety of *O. umbellifera* (L. ex Fr.) Quél. Fries's (1821) var.  $\beta$  is clearly *O. rustica* in our sense.

Redhead & Weresub (1978) consider, in our opinion wrongly, *Omphalina* as a nomen novum for *Omphalia* (Fr.) Quél. and consequently think that *Omphalina* and *Omphalia* must have the same type. They reject *A. umbelliferus* L. ex Fr. as type for *Omphalina* and for *Omphalia* ("Pers. ex Fr.") because it was accepted by Fries 1821 only as synonym, and even that is a misinterpretation of *Agaricus umbelliferus* Linnaeus, Scop. etc., and as far as the latter generic name is concerned we must agree with them. They propose instead, and apparently logically so, that *A. epichysium* Pers. ex Fr. should then be the type species of this genus. "If all authors had been privy to our current Code of Nomenclature this species would undoubtedly have been chosen as the type species." (I.c. p. 565). *A. umbelliferus* L., With. ex Hooker is *Mycena capillaris* according to Fries.

Lange (1981) also proposes *O. umbellifera* (but sensu *Omphalina ericetorum* (Fr. ex Fr.) Sing.) as the type species for *Omphalina*. This choice is unacceptable (1) because it is a later choice than mine and the acceptable first choice of lectotype must be followed. (2) It is based on Fries, *Elenchus* 1: 22. 1828; Linnaeus' fungus diagnosis is quoted together with (in second place) *A. ericetorum* S.M. 1: 165. where the species is understood in a broad sense. (3) Quélet's (1886) protologue sets *A. pseudoandrosaceus* Bull. in parenthesis as an explanation of his interpretation of the preceding citations which becomes clear in his emended description of 1888. There are further misleading statements in Lange's discussion. The authentic Persoon material studied by me at L (no. L 910.256-1888) is indeed, unfortunately, not completely described but if it does not have incrusting pigment it could not be a lecto- or isotype because Persoon's original description is quite clearly an *Omphalina* ("Totus griseus..." *Synopsis* p. 472. 1801.) in our sense.

spored; cystidia none but narrow cheilocystidia at times present; hymenophoral trama irregular to more rarely regular and then very narrow and partly replaced by a broad irregular lateral stratum, the hyphae of the irregular trama often ± opaque and somewhat thick-walled, inamyloid; stipe fleshy to subcartilaginous, narrowly hollow or stuffed, becoming hollow, 1-2, only exceptionally more millimeters thick, central; black rhizomorphs none; context often hygrophanous, watery, thin, often partly consisting of somewhat thick-walled hyphae, with or without clamp connections. On rocky soil, on sand, on dead wood, buried wood, on or among mosses, often lichenized.

*Development of the carpophores:* Gymnocalypous, stipitocarpous (Watling 1985). Often parthenogenetic.

*Area:* Only in the extratropical zones and in semi-arid and alpine regions of the mountains in the tropical-subtropical belt, reaching both the alpine and the arctic and antarctic zone.

*Limits:* The delimitation of this genus against *Clitocybe* has been discussed in that genus. *Omphalina* can be distinguished from *Armillariella* by the size of the carpophores; the smallest representative of the latter (*A. saviczii*) has black rhizomorphs and an annulus.

*Hygroaster* differs in star-shaped-spinose spores. The pink-spored section of *Omphalina* differs from other pink-spored Tricholomataceae by the omphalioid habit correlated with presence of clamp connections and incrusting pigment. *Gerronema* differs constantly in the absence of intraparietal and incrusting pigment on the normal (as contrasted with oleiferous) hyphae. Aside from the difference in pigments, the species of *Gerronema* also have a different ecology and area (forest-inhabiting, often tropical whenever devoid of yellow or carotenoid pigments). As for the delimitation of *Leptoglossum*, see the latter genus.

*State of knowledge:* There are now 32 species admitted in *Omphalina*.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *OMPHALINA* (Genuinae Romagn. 1942). Tramal hyphae with clamp connections. Spore print white. Exceptional bisporous forms of *O. pseudoandrosacea* without clamps.

*Type species:* *O. umbellifera* (L. ex Fr.) Quél. sensu Quél. (= *O. pseudoandrosacea*).

*O. griseopallida* (Desm.) Quél. (*O. griseola* (Pers.) Quél.); *O. obscurata* Reid; *O.lundellii* (Pilát & Nannfeldt) Bresinsky; *O. obatra* (Favre) Sing.; *O. subobscura* Sing.; *O. subandina* Sing. (*O. subumbratilis* Sing. non Murr.); *O. chilensis* (Mont.) Sing.; *O. mostnyae* Sing.; *O. antarctica* Sing.; *O. pseudoandrosacea* (Bull. ex St. Amans) Moser in Gams (*O. grisella* (Weinm.) Moser in Gams; *O. umbellifera* (L. ex

Fr.) Quél. sensu Quél. (non Fr.); *Omphalina baeospora* Sing.; *O. muralis* (Sw. ex Fr.) Sing. (= *O. pseudomuralis* Lamoure *Trav. Sc. Parc Nat. Vanoise* 5: 155. 1974); *O. trigonospora* Lamoure; *O. epichysium* (Pers. ex Fr.) Quél.; *O. fusconigra* Orton; *P. philonotis* (Lasch) Quél. (sensu Favre); *O. sphagnicola* (Berk. im W.G. Smith) Moser apud Gams; *O. gerardiana* (Peck) Sing. (if different from the two preceding species); *C. columbiana* Sing.; *C. umbratilis* (Fr.) Quél. and var. *minor* (Fr.) and var. *depauperata* Sing. & Clém.; *O. pyxidata* (Bull. ex Fr.) Quél. with var. *pluviarum* Sing. & Digilio and var. *rivilicola* (Favre) and f. *bispora* Sing. (ined.); *O. hepatica* (Fr.) Orton; *O. chlorocyanea* (Pat.) Sing.\*.

Sect. 2. *RHODOMPHALINA* Pouzar in Svrček & Kubička (1971). Tramal hyphae with clamp connections; spore print pink.

Type species: *O. lilaceorosea* Svrček & Kubička.

*O. demissa* (Fr.) Quél.; *O. lilaceorosea* Svrček & Kubička; *O. discorosea* (Pilát) Herink & Kotlaba (*Rhodocybe xylophila* Vasilkov).

Sect. 3 *DEFIBULATAE* Sing. (1975). Tramal hyphae constantly without clamp connections; spore print white.

Type species: *O. defibulata* Sing.

*O. rustica* (Fr.) Quél. (sensu Bres.) (*A. ericotorum* Pers. non Fr.); *O. oreades* Sing. (*Clitocybe albimontana* Bigelow); *O. telmatiae* (Berk. & Cooke) Dennis ex Sing.; *O. defibulata* Sing.; also *Omphalia anthodia* (Pers.?) Lundell, FES 1752.

### 34. **GERRONEMA** Sing.

*Mycologia* 43: 599. 1951.

Type species: *Gerronema melanomphax* Sing.

Syn.: *Haasiella* Kotlaba & Pouzar, *Cesk. Mykol.* 20: 135. 1966.

*Omphalia* Kummer, *Führ. Pilzk.*, p. 26. 1871, non S.F. Gray, nec (Fr.) Quél. nec *Omphalea* Linn. (1759).

*Rickenella* Raitelhuber, *Metrodiana* 4: 67. 1973.

*Chrysomphalina* Haas, *Zeitschr. Pilzk.* 28: 13. 1962 ex Clémenton, *Zeitschr. f. Mykol.* 48: 202. 1982.

*Chrysobotrychodes* Kost, *Zeitschr. f. Myk.* 51: 246. 1985

**Characters:** Habit omphalioid (the largest forms appearing almost clitocyboid and/or vaguely pleurotoid); pileus and stipe pigmented, or if not pigmented (white) hyphae without clamp connections; if pigmented, pigments never intraparietal nor incrusting (intercellular on specialized hyphae in some tropical forms); xanthinid (yellow) or carotenoid pigments frequently present particularly in the temperate species, generally present in subgenus *Romagnesia*; hyphae monomitic, mostly filamentous but in most species somewhat, in some strongly\*\* inflated but in others

\**A. smaragdinus* Berk. often quoted as conspecific with *O. chlorocyanea* is not an *Omphalina* but a *Marasmius*.

\*\*Clémenton (1982) indicates that the species of *Rickenella* (= sect. *Fibulae*) differ from those of *Gerronema* by having broad, at the septa constricted, "physalo-hyphae" in the hymenophoral trama. This

rather variable in this regard and not fully corresponding to Corner's sarcodimitic type but the inflated hyphae although often cylindrical not reaching extraordinary length between septa, mostly thin-walled, but in some species in parts tending to be slightly thick-walled, sometimes densely interwoven, in other species tending to be remarkably loosely arranged, inamyloid, with or without clamp connections; spore print varying from white to yellow or orange, sometimes a very pale greenish citrine; spores hyaline to palest yellowish in KOH, and then often metachromatic in cresyl blue mounts, inamyloid, acyanophilous, rarely a few spores cyanophilous (intermixed with acyanophilous ones) with thin, homogeneous wall, sometimes slightly thickened; basidia mostly tetrasporous not elongated nor with siderophilous granulation; basidioles not fusiform; cystidia and dermatocystidia generally absent (present only in species without clamp connections and/or carotenoid pigments, but cheilocystidia present in some tropical species. Lamellae decurrent, mostly rather narrow; hymenophoral trama regular or subregular (often soon rather strongly interwoven hyphae present, but also often with parallel hyphae especially in the mediostratum and near the edge of the lamellae. Veil none. Cortical layers little differentiated, with repent, more rarely in places somewhat ascendant, smooth, filamentous hyphae, forming a cutis, more rarely a thin trichodermium, rarely a well developed, deep trichodermium; context whitish or concolorous with the surfaces, usually unchanging, but some (tropical species) showing a strong tendency to become reddish chestnut or chestnut red in age and on drying. On decayed wood and on mosses and Hepaticae or directly on earth, often lichenized (see in chapter on Lichenization, p. 13 and under "Development of the carpophores" below) in subgenus *Romagnesia*.

*Development of the carpophores:* Gymnocarpous in *G. icterinum* (Singer) and *G. chrysophyllum* (Blizzard). - In some species the carpophores represent the fructification of a basidiolichen (either *Botrydina* or *Coriscium*, see also on p. 13, 277).

Lichenization is particularly common in the species without clamp connections of the temperate zone but I was unable to corroborate Gams' statement regarding the lichenization of *G. fibula* in alpine habitats. In *G. schusteri* from Antarctica, in *G. postii*, *G. marchantiae*, *G. venustissimum* and *G. splendidissimum* all carpophores checked were non-lichenized. In South American species, also occurring in the arctic, subarctic and alpine zones, the lichen thallus appears to be not constant for a species (cf. Singer in *Flora Neotropica* 3: 72-74. 1970). On the other hand, *Botrydina*-thalli are also found to occur in *Omphalina* (clamp-less parthenogenetic form of *O. pseudoandrosacea* and *O. rustica*), and even in *Aphylophorales* (Clavarioid and corticioid fungi). The algae are, in the case of *Gerronema*, representatives of the genus *Coccomyxa*. Although the association *Coccomyxa/Gerronema* appears to be constant and obligatory in nature, the morphological structure of the thallus is not constant if the world flora is considered, but it appears

observation expresses only one extreme of the very variable hyphal structure in sect. *Fibulæ* where only an (often small) portion of the hyphae is constricted, and the diameter of the broadest hyphae often reaches no more than 3-12 µm. Such hyphae can also be observed in some species of other sections of *Gerronema*.

to be constant in a given region. The association with aberrant lichen thalli may justify recognition of subspecies or, if the fungus shows constant differences, even (micro-) species.

Since lichenization is apparently confined to parthenogenetic forms - very common in *Omphalina* as well as *Gerronema* - it would seem that lichen-association depends more on the development of the fungus than on its taxonomic position in its respective genus.

**Area:** Tropical and subtropical America and Asia, also in temperate and frigid zones (Europe, North America, Southern South America and Antarctica, Northern and Eastern Asia); each subgenus with characteristic areas of distribution.

**Limits:** This genus differs clearly and sharply from *Omphalina* by its pigmentation. The pigments in *Gerronema* when seemingly incrusting, are either light or bright colored and either intercellular or thinly and slightly resinously incrusting and not dark colored but (in KOH) ochre to pale brownish. In either case they do not necessarily appear in the fresh adult specimens (they are suspected to be necropigments in some cases) or are confined to a conducting hyphal system or very young pilei (becoming dissolved in further development). *Gerronema* often has carotinoid pigments which do not occur in *Omphalina*. - As for subsection *Fibulae*, see under *Mycena*. *Gerronema* differs from *Clitocybe* by its omphaliod habit; the larger (slightly clitocyboid-appearing) forms always contain yellow or orange pigment or have no clamp connections, or else differ from the closest section in *Clitocybe* by not having any incrusting or intraparietal pigment. *Callistosporium* may at times appear to be anatomically and chemically similar, but it never has decurrent lamellae. *Lactocollybia* and *Macrocystidium* differ in the abundance of gloeo-cystidia and/or latex. While the genera compared above are obviously among the ones most closely related to *Gerronema*, there is also apparently an evolutionary line leading from *Gerronema* to the Leucopaxilleae (through *Pseudoarmillariella*, but this differs in amyloid spores and incrusting pigment) and Myceneae (through *Hydropus*). There is a subsection in *Hydropus* which shows smooth repent thin-filamentous epicuticular hyphae and inamyloid spores. This section should be compared with *Gerronema* (see also delimitation of *Hydropus*).

*Gerronema* has become an object of frequent complaints by European authors who claim that the genus is heterogeneous, which is understandable if only European species are considered. This opinion is supported by the fact that Bigelow (1970, 1982) recognizes it (as *Omphalina* sensu Bigelow) in America. Lamoure (1983 echoes Kühner's (1977) opinion; her own interesting data merely support the notion that sect. *Fibulae* is a well characterized, natural unit.

**State of knowledge:** The genus has been the subject of two revisions (Bigelow 1970, as *Omphalina*; Singer 1964, 1970), but additional species have been introduced since then. Including these, we now know 59 species belonging in *Gerronema*.

**Practical importance:** Unknown.

Sungenus 1. **Gerronema**. Pigment mostly present but never deep orange (rarely orange yellow in the lamellae and spores exclusively, but then the color of the pileus different at least in its larger portion) and spore print always white or perhaps pale cream when fresh; pigments of pileus not olive-ochraceous nor turning reddish chestnut or castaneous-red in age (if such pigments present, see subgenus II), and laticiferous or gloeo-vessels also absent (if present, see *Lactocollybia*); context soft-fleshy-membranous (in the stipe even subcartilaginous) to slightly toughish-fleshy; true cystidia mostly absent but cystidoid bodies at times present; hymenium sometimes poorly formed (not truly "hymeniform-palidadic"); hymenophoral trama regular but hyphae of unequal shape and diameter in some species, often with slightly thickened walls in trama of pileus and stipe and often also in the hymenophore: on rotting wood in forests, especially in the tropics and subtropics few species in the temperate zones.

*Type species: G. melanomphax* Sing.

Sect. 1. **UMBILICATA** (Sing.) Sing. (*Clitocybe* sect. *Umbilicatae* Sing. 1948). Pileus strongly hygrophanous, not innately fibrillose; yellowish pigments absent; clamp connections present. Temperate and subtropical-montane species.

*Type species: C. umbilicata* (Fr. Kummer (sensu Lange).

*G. umbilicatum* (Fr.) Sing. (sensu Lange f. *subspadicea* Lange) (*Clitocybe*, Kummer; *Omphalia*, Quél.); *G. oligophyllum* (Sing. in Sing. & Digilio) Sing.; *G. aconquijense* (Sing. in Sing. & Digilio); *G. moseri* Sing.; according to Cléménçon also *G. nitriolens* (Favre) Cléménçon.

Sect. 2. **XANTHOPHYLLA** Sing. (1961). Pileus not or not strongly hygrophanous, mostly distinctly innately fibrillose-striped or radially fibrillose; yellowish pigment often present. Clamp connections present in 4-spored carpophores. Few species passing into the humid-warm temperate zone (both North and South), most restricted to the intertropical and subtropical zones.

*Type species: G. icterinum* (Sing.) Sing.

*G. elasticum* Sing. with ssp. *amazonicum* Sing.; *G. hypolepargum* Sing.; *G. theophili* Sing.; *G. leptosarcum* Sing.; *G. majus* Sing.; *G. xanthodictyon* Sing.; *G. suboreades* (Beeli) Sing.; *G. calongei* Sing.; *G. cheilocystidiatum* Sing.; *G. strombodes* (Berk. & Mont.) Sing.; *G. hypoxanthum* (Bres. & Cav.) Sing. (*Omphalia hypoxantha* Bres. in Bres. & Cavara N. Giorn. Bot. It. n.s. 8: 18. 1901; *O. bresadolae* Maire); *G. subclavatum* (Peck) Sing. (*Omphalina lenta* Murr.; *G. subchrysophyllum* (Murr.) Sing.); *G. icterinum* (Sing.) Sing. (*Omphalina euomphalus* var. *lutea* Dennis); *G. retiarium* (Berk.) Sing.; obviously also *Clitocybula dryadicola* Kühn.

Sect. 3. **GERRONEMA**. Pigments present at least in the center of the pileus, or without pigments at all, without yellowish pigments in the lamellae; hyphae without clamp connections and 4-spored basidia present. Two species European, all others tropical and subtropical.

Type species: *G. melanomphax* Sing.

*G. albidum* (Fr.) Sing.\* (*Cantharellus*, Fr.; *Hygrophoropsis*, Maire; *Valentinia vacini* Velen.); *G. alutaceum* Sing.; *G. subpallidum* Sing.; *G. clavuligerum* (Sing.) Sing.; *G. angustifolium* Sing.\*\*; *G. melanomphax* Sing.; *G. depauperatum* Sing.; *G. minutissimum* Sing. - Here: *G. collybiomorphum* Sing.\*\*\*.

Subgenus II. **Romagnesia** (Sing.) Sing. (1961: *Omphalina* subg. *Romagnesia*, 1947). A yellow, pink, or orange (carotenoid) pigment present, or a chestnut-red to chestnut pigment becoming apparent in age, on drying, or with KOH, rarely pileus and lamellae with little or no such pigment and then stipe at least in part bright brown, yellow, lilac, or deep violet; trama often pigmented, in alkalic media oleiferous hyphae often strongly pigmented, these pigments in the non-oleiderous hyphae generally intracellular, rarely, especially in specialized hyphae such as oleiferous hyphae, intercellular or incrusting, often dissolved into the (alkalic) medium; context somewhat tough only in the tropical species of sect. 4, otherwise fleshy and fragile, rapidly putrescent. Spore print white to yellow, cream, or orange; hymenium well formed; hymenophoral trama regular to subregular, sometimes more axially arranged in part of the mediostratum, mostly most hyphae quite thin-walled, or some moderately thick-walled ones present, filamentous or somewhat inflated; cystidia present or absent; clamp connections present or absent; epicutis - a cutis of smooth hyphae, but in the cystidiate species dermatocystidia usually abundant on both pileus and stipe. On dead wood and in deep moss, among Hepaticae and in *Sphagnum*, more rarely on various plant débris, on soil or humus. Species of the temperate and frigid, more rarely the subtropical and tropical zone especially in the "páramo" and "subpáramo".

Type species: *Omphalina postii* (Fr.) Sing. (= *G. postii* (Fr.) Sing.).

Sect. 4. **CYATHIFORMIA** Sing. (1961). Clamp connections present; cystidia absent; pileus neither bright yellow or orange nor pink; context somewhat toughish; carpophores becoming chestnut to chestnut-red in age, on drying, and/or by remoistening with alkali. All species tropical and subtropical, generally lignicolous, or on débris.

Type species: *G. cyathiforme* (Berk. & Curt.) Sing.

*G. cyathiforme* (Berk. & Curt.) Sing. (*Marasmius*, Berk. & Curt.); *G. bryogeton* Sing.; *G. brunneum* Sing.; *G. stuckertii* (Speg.) Sing. apparently also *G. holochlorum* (Berk. & Br.) Pegler (*Omphalia*, Sacc.; *Trogia*, Corner).

\*The correct name of this species in our (including Kühners') sense is, according to Redhead (1984): *G. prescottii* (Weinm.) Redhead.

\*\*No 4-spored form has been discovered until now. This species should probably be transferred to sect. *Xanthophylla*.

\*\*\*In the original diagnosis (*Schw. Zeitschr. Pilzk.* 56: 155. 1978) is stated "hyphis... fibulatis". Intended was "hyphis... defibulatis". This species will key out in *Lulesia*, but the status of the type species of that genus, not restudied by me, should be clarified before a transfer of *G. collybiomorphum* is considered.

Sect. 5. *CHRYSOPHYLLA* Sing. (1964). Carotenoid pigments present, but other dark-colored pigments also often present. Spore print orange, orange yellow, or orange-salmon ("pinkish-buff" to "warm buff" or "salmon buff" to "ochraceous salmon" Ridgway, according to Bigelow); spores not metachromatic in cresyl blue mounts, relatively large ( $>10 \mu\text{m}$ ). Species of the temperate zone, lignicolous.

Type species: *G. chrysophyllum* (Fr.) Sing.

*G. chrysophyllum* (Fr.) Sing. (Omphalia, Kummer; Omphalina, Murr.; Clitocybe luteophylla Bigelow & Hesler); apparently also *Omphalina hoffmannii* (Peck) Bigelow.

Sect. 6. *ROMAGNESIA*. Characters different from those of sect. 4 and 5: Xanthinic and carotenoid pigments almost always abundant, exceptionally olive exclusively but pigments not staining chestnut in KOH, not intercellular, but often dissolved by the alkalic medium; cystidia and/or dermatocystidia, none; clamp connections present or absent; spores metachromatic or not in cresyl blue medium; often lichenized; context of pileus and stipe fleshy to fleshy-membranous, fragile. Species of the frigid and temperate zones, more rarely the subtropical zone, lignicolous or terricolous, but most frequently growing among mosses (*Polytrichum*, *Bryaceae*, *Sphagnum*) or Hepaticae or lichens, often in groups.

Type species: *G. postii* (Fr.) Sing.

Subsection *Porpophora* Sing. (1964). With clamp connections.

Type species: *G. dennisii* Sing.

*G. brevibasidiatum* Sing. (Omphalia cincta Favre); *G. luteicolor* (Murr.) Sing.; *G. infundibuliforme* Sing.; *G. dennisii* Sing.; *G. tenue* Dennis; *G. pseudomurale* (Speg.) Sing.; apparently also *Omphalia sphagnophila* Peck.

Subsection *Venustissima* Sing. (1964). Without clamp connections.

Type species: *G. postii* (Fr.) Sing.

*G. postii* (Fr.) Sing.; *G. marchantiae* Sing. & Clémenton; *G. hudsonii* (Jennings) Sing.; *G. alpinum* (Britz.) Bresinsky & Stangl (*G. luteovitellinum* (Pilát & Nannf.) Sing.); *G. grossulum* (Pers.) Sing.; *G. ericetorum* (Fr. ex Fr.) Sing. (Omphalina, M. Lange; Merulius turfosus Pers.; non A. ericetorum Pers.); *G. infumatum* (B. & Br.) Sing.\*. Additional races or microspecies differing mainly in the association with different lichen thalli may be admitted.

Sect. 7. *HAASIELLA* (Kotalaba & Pouzar) Sing. stat. nov. (*Haasiella* Kotlaba & Pouzar l.c., ut genus). Differs from sect. *Romagnesia* in the thicker wall of the spores which includes a red-metachromatic endosporium when studied in cresyl blue or toluidin blue mounts. Spore print pale yellowish salmon; cystidioles often present, but cystidia and dermatocystidia none; clamp connections present or absent.

\*c.n. (*Agaricus infumatatus* Berk. & Br., *Ann. Mag. N.H.V.* 1: 125. 1881).

*Type species: H. splendidissima* Kotlaba & Pouzar.

*G. splendidissimum* (Kotlaba & Pouzar) Sing.; *G. venustissimum* (Fr.) Sing.; *G. macrosporum* (Sing.) Sing.

Sect. 8. *FIBULAE* (Sing.) Sing. (1961). Differs from the preceding sections mainly in the presence of pleuro- and dermatocystidia. The orange or yellow pigment may be very scarce or absent, but then the stipe is either lilac or dark violet at the apex, or a pink or olive pigment present in the lamellae or on the pileus. Generally not lichenized species of the temperate zones of the Northern and Southern Hemisphere.

*Type species: M. fibula* (Bull. ex Fr.) Sing. (*Gerronema*, Sing.).

*G. fibula* (Bull. ex Fr.) Sing.; *G. schusteri* Sing.; *G. melleum* Sing. & Clémenton\*; *G. pseudogrisellum* (Smith) Gulden & Lange; *G. setipes* (Fr.) Sing. (A fibula var. *swartzii* Fr.); *G. alexandri* Sing.; *G. cotopatae* Sing.; *G. rosellum* (Lange) Sing.\*\*; *G. versatile* (Bert. & Mont.) Sing.; obviously also *Rickenella demisella* (M. Lange) Clémenton.

Subgenus III. *Quetria* Sing. (1964). Pigment present on the pileus, but neither olive, nor pink, nor yellow nor orange nor chestnut; cystidia present; clamp connections absent: spore print white. Temperate species of the Southern Hemisphere.

*Type and only species: G. minutum* (Sing. & Digilio) Sing.

### 35. **CALLISTOSPORIUM** Sing.

*Mycologia* 36: 363. 1944.

*Type species: Gymnopus palmarum* Murr. [= *Callistosporium palmarum* (Murr.) Sing.].

*Characters:* Habit of the carpophores collybioid; pigment present, abundant, changing its color in dried condition, mostly concentrated in solid (or sometimes dissolved) pigment bodies inside the spores, and also often in other elements of the hymenophore where the pigment is colorless under the microscope in fresh condition but precipitates on dehydration; pileus hygrophanous or non-hygrophanous, its cuticle consisting of repent, elongate hyphae sometimes with peg-like hyphal bunches arising from them; hymenophore lamellate, lamellae subdecurrent to narrowly adnexed or emarginate; spore print white when fresh; spores ellipsoid, smooth, inamyloid, at least a certain percentage of the spores usually partly bright colored (the interior of the spores) in dried specimens, or rarely with a hyaline pigment body, with thin, hyaline walls, uninucleate, scarcely or weakly cyanophilic; basidia normal but sometimes some of them pigmented the same way as the spores;

\* Redhead (1980) and others identify *Omphalina demisella* M. Lange, *Gerronema melleum* Sing. & Clémenton, and *Mycena pseudogrisella* as being forms of the same species. While they seem to have similar substrata, they must be enormously variable in several essential characters such as spores size and shape, colors, shape of cystidia, and attachment of the lamellae if, indeed, they were all three conspecific.

\*\* According to British material (C 5305, F); type not seen.

cystidia of all types absent; hymenophoral trama regular, inamyloid; stipe central, thin, fleshy-fragile, to subcartilaginous; context not tough, nor reviving, consisting of hyphae without clamp connections. On the base of palm trees and on various kinds of wood, also on *Sphagnum*, and on the earth.

*Development of the carpophores:* Not studied.

*Area:* In the Asiatic subtropics and tropics and in America from the tropics to the boreal zone (Canada), south to Argentina, also two species in Europe.

*Limits:* The peculiar pigmentation of the spores which can be considered as constant, is undoubtedly an easy way of recognizing this genus among all other *Omphalinae*. This genus differs from *Tricholoma* not only because of the necro-pigment of the spores and/or some hymenial cells but because of its habit which is generally collybioid with thin, early tubular-hollow, fragile or subcartilaginous stipe and mostly differently attached lamellae, and the decidedly non-ectotrophic mycelium which differentiates this genus from all clampless species of *Tricholoma*. Kühner's attempt (1980) to include *Callistosporium* (and even *Dermoloma*) in *Tricholoma* must be attributed to his wide concept of genera in Agaricales.

*State of knowledge:* At least 10 species belong in this genus.

Our knowledge on the species here definitely recognized is quite satisfactory. A key to the species has been published (*Sydotia* 30: 261-264. 1977) where *C. majus* Sing. must be replaced by *C. xanthophyllum* (Malençon & Bertault) Bon.

*Practical importance:* Unknown.

## SPECIES

*C. palmarum* (Murr.) Sing.; *C. heimii* (Sing.) Sing.; *C. luteoolivaceum* (Berk. & Curt.) Sing.; *C. xanthophyllum* (Malençon & Bertault) Bon; *C. favrei* Sing.; *C. luteofuscum* Sing.; *C. amazonicum* Sing.; *C. terrigenum* Sing.; *C. chrysophorum* Sing.; *C. galerinoides* Sing.; obviously also *C. xerampelinum* Pegler and *C. graminicolor* Lennox.

*Note:* Redhead (1982) thinks that *C. luteoolivaceum*, *luteofuscum*, *luteofuscum* var. *majus* Sing., *C. elaeodes* (Romagnesi ex) Bon, *C. favrei* and *C. graminicolor* are conspecific. This conclusion is due to an extraordinarily wide species concept. Some of Redhead's nomenclatural views (e.g. on *C. xanthophyllum* (Mal. & Bert.) Bon) are certainly erroneous.

## 36. PLEUROCOLLYBIA Sing.

*Mycologia* 39: 81. 1947.

*Type Species:* *Pleurocollybia praemultifolia* (Murr.) Sing.

*Characters:* Habit pleurotoid, more rarely collybioid, but pileus always, even if

eccentrically or non-stipitate, like that of *Collybia*; spore print pure white; hymenophore lamellate, lamellae usually very thin and close to crowded, marginate-adnexed or sinuate, also adnate or with a slight decurrent tooth, or concurrent; lamellulae often abruptly truncate; stipe eccentric and often oblique or curved, more rarely central or absent, base of stipe with white basal mycelium; veil none; taste mild or bitter; covering of pileus none above a cutis-like epicutis which consists of filamentous hyphae, often multiseptate, smooth, rarely with scattered knob-like bulges, non-gelatinized; hymenophoral trama regular; hyphae inamyloid, typically without clamp connections but in a few species with scattered to rather numerous clamps; walls thin or firm, not strongly thickened; subhymenium present, subcellular, of minute, short elements; trama absolutely monomitic, many hyphae inflated, without gelatinization; spores small (<6 µm, often minute), hyaline, with smooth, inamyloid, weakly to distinctly cyanophilous wall; basidia small, normal, or extremely small; cystidia none; cheilocystidia, if present, not making the edge of the lamellae heteromorphous, not very conspicuous, often occurring in bunches. Pigments not incrusting, brown, fuscous, beige, pinkish cinnamon ?lilae. On rotting wood, more rarely on herbaceous rests or on leafmold, the strictly pleurotoid carpophores always found on wood.

*Development of the carpophores:* Unknown.

*Area:* From warm-temperate America to the tropics and south to Southern Chile; also in Africa.

*Limits:* This genus differs from *Tricholoma* by its habit, and even the centrally stipitate forms differ from the thinner *Tricholomas* (section *Adusta*) in not being ectotrophically mycorrhizal and in having intracellular pigment. *Podabrella* differs in pink spore print and siderophilous basidia. The clampless *Gerronemas* have ± decurrent lamellae, with attenuated lamellulae. *Callistosporium* differs in central stipe and different pigments, particularly in the characteristic necropigment of the spores. *Collybioid* species should be compared with *Collybia* (p. 313-318).

*State of knowledge:* Eight species are fully known, except for their sexuality and development of the carpophores.

*Practical importance:* One species is commonly eaten in Perú.

## SPECIES

### 1. Typical species without clamp connections:

*P. praemultifolia* (Murr.) Sing.; *P. brunnescens* (Earle) Sing.; *P. densifolia* (Murr.) Sing.\*; *P. cibaria* Sing.; *P. pulcherrima* Sing. ined. *P. apoda* Sing.

### 2. Atypical species with clamped septa\*\*.

\*c.n. (*Gymnoporus densifolius* Murr., *N. Am. Fl.* 9: 371. 1916)

\*\**P. cibaria* Sing. has, in some collections, a few clamp connections, an observation which confirms the presence of clamps in some species of *Pleurocollybia* (cf. Singer 1970, p. 50-55) and the impossibility to base sections on presence or absence of clamps.

*P. amara* (Murr.) Sing.; *P. paradoxa* Sing. Possibly here: *Collybia syringea* Sing.

Note: *Lentinellus cremeus* Stevenson from New Zealand was transferred to *Pleurocollybia* by Horak (1971) who however indicated "weakly amyloid" spores, and to *Omphalina* by O.K. Miller (1971) who indicated inamyloid spores. Neither author reported clamp connections.

### 37. LACTOCOLLYBIA Sing.

*Schweiz. Zeitschr. f. Pilzk.* 17: 71. 1939.

Type species: *L. lacrimosa* (Heim) Sing.

Syn.: *Bertrandiella* Heim, *Rev. d. Mycol.* 24: 192. 1959.

**Characters:** Habit of the carpophores mostly collyboid, more rarely pleurotoid or mycenoid or omphalioid; pileus not viscid and more or less hygrophanous or non-hygrophanous; lamellae well developed, adnexed to adnate or decurrent; stipe well developed, but in one species eccentric, not insititious, rarely subinsititious; a slight veil present, or more often absent, never forming an annulus. Latex often present. Spores of various shapes, smooth, inamyloid, acyanophilic, thin-walled, white or cream, not pinkish in print. Basidia 2- or 4-spored, normal. Gloeocystidia (Pl. 21,3) present; cheilocystidia scattered to numerous, rarely absent. Hyphae with or without clamp connections; subhymenium cellular or ramosc; pigments present and abundant (in one section greening with alkali), or scarce to absent; hymenophoral trama regular, not gelatinized, consisting of parallel or subparallel hyphae and (often) gloeo-vessels (Pl. 33,2); epicutis consisting of a non-gelatinized cutis, or merely dense, with superimposed or deep-rooting gloeocystidia which are scarce to (mostly) numerous, sometimes in connivent fascicles, rarely absent; dermatopseudocystidia (gloeocystidia) also often present on the stipe. On earth, leafmold, wood, living plants (on living cortex of trees, on Cycads, on fallen fruits) and various débris.

**Development of the carpophores:** Unknown.

**Area:** Tropical and subtropical, rarely entering the warm-temperate zone in North America and Chile; also in India and tropical Africa.

**Limits:** This differs from the lactescent species of *Mycena* in the inamyloid spores. The genus is obviously most closely related to *Macrocytistidia* from which it differs in white spore print and acyanophilic spore walls (sometimes these may appear slightly cyanophilous because a cotton-blue-absorbing zone appears on the inner surface of the wall whereas in *Macrocytistidia*, the cyanophilic layer is the outer layer of the spore wall). Not all species for which the spore print color is unknown, have been rechecked for cyanophily. In *Lactocollybia*, the spore wall is acyanophilic (in *L. angiospermarum* and *L. ianthina*).

In *Gerronema macrosporum* numerous elements are filled with an orange substance, including the basidia and spores, but no gloeocystidia have been observed.

*State of knowledge:* 13 species are well known.

*Practical importance:* Some species are parasitic at times, but the damage inflicted seems to be of minor importance; at least no diseases on cultivated plants are known to be caused by *Lactocollybia*. *L. aequatorialis* is used as food by the Sanama in the Amazonian region of Brazil.

## SPECIES

Section 1. *BERTRANDIELLA* (Heim) Sing. (*Bertrandiella* Heim ut gen., *l.c.*). Subhymenium subcellular, of very short elements; latex very scanty, often nearly absent; pigment violet, but surfaces soon bleaching; young carpophores with a thin, fugacious veil. Clamp connections present. Not lignicolous.

Type and only species: *L. ianthina* (Heim) Sing.

Section 2. *LACTOCOLLYBIA* (*Lacrimosae* Sing. 1952). Subhymenium ramosa (according to Heim); latex watery. Clamp connections none observed (according to Horak); laticiferous hyphae abundant, passing onto the edges of the lamellae as pseudo-(gloeo-?) cystidia; veil none. Lignicolous.

Type species: *L. lacrimosa* (Heim) Sing.

*L. lacrimosa* (Heim) Sing.; perhaps also *M. atroviolacea* Heim.

Section 3. *ALBAE* Sing. (1952). Subhymenium subcellular to almost ramosa, but its elements multiseptate; latex none. Clamp connections present. Gloeocystidia numerous on the sides of the lamellae and the surface (or only on the surfaces and scanty on the lamellae; or vice versa); veil none. Both on the ground on débris, and on wood (living and dead), on cycads, fallen fruits etc. Pigment either none, or not bright (not violet).

Type species: *L. cycadicola* (Josserand) Sing.

*L. cycadicola* (Joss.) Sing.; *L. aequatorialis* Sing.; *L. angiospermum* Sing.; *L. microspora* Sing. (if not too close to "Pleurotus luteoaurantius" - described as yellow-orange); *L. modesta* Sing.; *L. holophaea* (Mont.) Sing.; *L. albida* (Murr.) Sing.\*; *L. marasmiiformis* (Murr.) Sing.\*\*; *L. carneipes* (Speg.) Sing.\*\*\*.

Section 4. *AURANTIACAE* Sing. (1952). Differs from the preceding section in orange pigment, with in KOH greening gloeocystidia and in the absence of clamp connections. Latex none. Veil none. On the ground and on rotten wood.

Type and only species: *L. aurantiaca* Sing. in Sing. & Digilio.

Section 5. *GRAMINICOLAE* Sing. ined. Differs from the preceding sections in strongly pleurotoid habit and a distinct gelatinous layer underneath the epicutis

\*c.n. (*Gymnopus albidus* Murr., *Bull. Torr. Cl.* 66: 32. 1939.)

\*\*c.n. (*Gymnopus marasmiiformis* Murr., *N. Am. Fl.* 9: 371. 1916.)

\*\*\*c.n. (*Omphalia carneipes* Speg., *Bol. Acad. Nac. Cienc. Cordoba* 23: 377. 1919.)

which is a trichodermial palisade; clamp connections absent.

*L. graminicola* Sing. ined.

### 38. MACROCYSTIDIA Heim ex Josserand

*Bull. Soc. Myc. France* 49: 376. 1934.

*Type species:* *M. cucumis* (Pers. ex Fr.) Heim.

*Syn.:* *Macrocytis* Heim, *Le Genre Inocybe*, Paris, p. 71, 1931, non Agardh

*Galeromycena* Velen., *Nov. myc. nov.*, p. 66. 1947.

*Naucoria* sect. *Macrocytis* Konr. & Maubl., *Icon. Sel. Fung.* 6: 200. 1924-37.

*Agaricus* subgenus *Hypomnema* Britz., *Hym. Südb.* 3 b, *Ber. Naturh. Ver. Augsburg* 27: 196. 1883.

*Characters:* Habit of the carpophores collybioid or almost mycenoid; pigment present; pileus non-viscid, glabrous, hygrophanous, campanulate with recurved margin; lamellae subfree, thin; spore print ocher-reddish (pink); spores pale stramineous pink under the microscope, smooth, attenuate toward the apex, ellipsoid-oblong, with seemingly simple but slightly thickened wall, inamyloid; uninucleate, smooth under the light microscope, but uniformly rugulose under the scanning microscope according to Pegler & Young, outer wall layer cyanophilous; basidia comparatively small, otherwise normal; gloeocystidia voluminous, ventricose, often subglobose, later elongate, thin-walled, hyaline; hymenophoral trama regular; cuticle consisting of repent filamentous hyphae with numerous large dermatogloeocystidia forming a fragmentary epicutis; stipe central, rigid, but slender, without a pseudorrhiza, glabrous, beset with dermatocystidia; context colored, not tough in the pileus, without gelatinized portion; trama inamyloid; hyphae with clamp connections. On herbaceous sticks, wood, and on earth.

*Development of the carpophores:* Unknown.

*Area:* Temperate and tropical zone, especially in Europe and South America, Asia and Africa.

*Limits:* *Macrocytidia* is closely related to *Lactocollybia*. This is the reason why it is now inserted in subtribus *Omphalinae* in spite of the fact that all known species have clamp connections. The ultrastructure of the spore wall is certainly different from that of *Lactocollybia* but also from that of *Rhodocybe*. It is not unique in the Tricholomataceae (cf Horak 1980,, p. 1 compared with our pl. 53 A!).

*State of knowledge:* Six species are recognized.

*Practical importance:* None.

#### SPECIES

*M. cucumis* (Pers. ex Fr.) Heim [Agaricus, Fr.; Naucoria, Gillet; Macrocytis, Heim; Nolanea pisciodora (Cesati) Gillet; Agaricus piceus Kalchbr; Galeromycena

*mirabilis* Velen.]; *M. reducta* Horak; *M. indica* Saini, Atri & Sing.; *M. occidentalis* Sing. in Sing. & Digilio; *M. africana* Sing.; *M. incarnata* Sing.

### 39. FISSOLIMBUS Horak

*Sydowia* 8: 202. 1979.

*Type species: Fissolimbus fallaciosus* Horak.

**Characters:** Habit pluteoid-collybioid; spore print not white, apparently in color similar to that of the preceding genus; hymenophore lamellate, lamellae adnexed to free; stipe at base broader-bulbous or with a margined bulb, and with a ± viscid, rimose to pectinate margin in the type species; spores in KOH stramineous and smooth, (11.5)-12.5-16.5-(20) × (6)-6.8-8.5-(9.5)  $\mu\text{m}$ , not or only vaguely (in superposition) pseudoamyloid, not amyloid, the outer wall layer cyanophilic, without germ pore or callus, with homogeneous but double wall; basidia more often ventricose than clavate, tetrasporous (the giant spores occurring rarely but always on the same basidium as the others i.e. with three normal spores), without basal clamp, up to 47  $\mu\text{m}$  long; cystidia occurring on edges and sides of lamellae, large (to 84  $\mu\text{m}$  long), in KOH with seemingly homogeneous contents but in cresyl blue mounts with amorphous or coarsely banded blue to deep blue contents but with hyaline wall (gloeocystidia), non-incrusted, usually fusoid, also ampullaceous, rarely subcapitate, with rounded tip; hymenophoral trama regular, not gelatinized, consisting of mainly filamentous, always inamyloid hyphae without clamp connections; distinct gloeo-vessels rare, but oleiferous hyphae 2.5-5  $\mu\text{m}$  broad rather numerous; epicutis of the pileus - a cutis consisting of hyphae similar to those of the hymenophoral trama, on the umbo in places erect, and broader; pigment brownish, incrusting some hyphal elements of the epicutis; hypodermium little differentiated. On the ground in anecotrophic forests under *Araucaria*, among leaves.

**Development of the carpophores:** Unknown.

**Area:** New Guinea.

**Limits:** The large gloeocystidia, cyanophilic spores with off hyaline, smooth walls and the structures of the carpophores suggest affinity with *Macrocyptidia* with which it also shares most other characters. It differs principally in the pectinate margin, the bulbous stipe, and the lack of clamp connections. Horak considered this to be cortinariaceous. It is similar but obviously not related to *Inocybe*. The affinity with *Macrocyptidia* and the occurrence in anecotrophic forests do not favor insertion of *Fissolimbus* in the Cortinariaceae, but comparison with *Hebelomina* is indicated.

**State of knowledge:** Only the type species is known. Thanks to the amability of the author of the genus; material of the type has been studied by me.

**Practical importance:** Unknown.

*F. fallaciosus* Horak.

#### 40. ASPROINOCYBE Heim

*Rev. Mycol.* 34: 343. 1970 ("1969"), em. Heinemann

*Type species: Leucoinocybe lactifera* Heim, *Cah. Maboké* 7: 83. 1969. nom. nud.  
 (= *Asproinocybe lactifera* Heim)

*Characters:* Habit collybioid-pluteoid, sometimes almost tricholomatoid; pileus grooved or smooth, glabrous; stipe solid; lamellae subfree, often ± lactescent; spores gibbous (in circumference somewhat similar to *Inocybe* spores), white in print, walls inamyloid; basidia clavate, generally 4-spored, without distinct siderophilous granulation, with or without clamped base; hyphae with or without occasional or numerous (but often difficult to observe) clamp connections; with laticiferous hyphae ± distinct, these often with distinct colored contents; not gelatinized. Cystidia absent or present as pseudocystidia: epicutis of the pileus - a cutis, consisting of smooth or incrusted hyphae. Pigments mostly blue or amethyst or purple, especially in the lamellae; hymenophoral trama regular. On earth and rotten wood, tropical.

*Development of the carpophores:* Unknown.

*Area:* Subtropical and tropical in Africa and South America.

*Limits:* *Asproinocybe* forms part of a group of genera (37-40) related to each other but differing in spore characters. The neotropical representative was originally described as *Rhodocybe* but Baroni (1981) pointed out, correctly, that it does not belong there. Since Heinemann (1977) emended *Aproinocybe* and studied its type species, it became obvious that this species belongs there rather than in *Omphaliaster* as Baroni suggested. The pigments of *Omphaliaster* are quite different from those of *Asproinocybe*; clamp connections are totally absent in the former and the spores more star-shaped than nodulose-tuberculate, the basidia relatively longer, and the area of distribution of the genus as a whole strictly boreal-alpine rather than tropical-subtropical. Even the aspect of the carpophores is different since the lamellae in *Asproinocybe* are mostly subfree and never decurrent nor is the habit omphalioid. It is also interesting that, for different reasons, Horak as well as Heim emphasized the *Inocybe*-like features of *Fissolimbus* and *Asproinocybe* respectively.

*State of knowledge:* Four species are now known to belong in *Asproinocybe*, two of them re-examined by me.

*Practical importance:* Unknown.

## SPECIES

*A. lactifera* Heim; *A. ianthinocystis* (Sing.) Sing.; obviously also *A. russulooides* Heinemann and *A. brunneolilacina* Thoen.

### Reduced series: 41. CYPHELLOSTEREUM Reid

*Beih. Nov. Hedwig.* 18: 336. 1965.

*Type species:* *Stereum pusiolum* Berk. & Curt.

*Syn.:* *Stereophyllum* Karst., *Hedwigia* 28: 190. 1889 (non Mitt. 1859).

?*Pseudolasibolus* Agerer, *Mitt. Bot. München*, 19: 279. 1983.

*Characters:* Habit pleurotoid or *Gomphus*-like, but minute, narrowed behind and almost sessile or more often with a lateral, rarely subcentral stipe, soft and thin-fleshy (but thicker than *Mniopetalum*); hymenophore either rudimentary or more often absent; if rudimentary; sublamellate or with somewhat canaliculate surface; trama monomitic, not gelatinized, hyphae without clamp connections, inamyloid; pigment absent or virtually so; spores broadly ellipsoid or ellipsoid, few somewhat curved, not angular, smooth, hyaline, inamyloid, acyanophilous. Cuticular layer moderately differentiated, consisting of ascendant hyphal strands, hyphae with rounded ends, forming a sort of trichodermium. Cystidia typically present, thin-walled, subulate but with rounded apex. Typically on living mosses (or in association with some other autotrophic spore plants).

*Development of the carpophores:* Unknown.

*Area:* Europe, America, Africa, Asia.

*Limits:* This genus has often been combined with *Leptoglossum* from which it differs sharply and amply because of habit, cystidia, and lack of pigments. It may be confused with *Mniopetalum* but differs in the structure of the sterile surfaces and the absence of clamp connections.

I am using the name *Cyphellostereum* only with great hesitation. I am not familiar with the type species, *C. pusiolum*, and suspect that it might not be congeneric, and perhaps not even tricholomataceous, but refrain from the erection of a new genus replacing *Stereophyllum* Karst. (preoccupied) for the time being at least until the relation between *Stereum pusiolum* and Karsten's genus is sufficiently cleared up. As for *C. laeve*, my own collections and analysis lead me to agree with Reid (1971) who thinks this species to be related to *Leptoglossum*. If indeed the type of the genus is congeneric with the genus as admitted here (based on *C. laeve*), there is only one step further to include *Pseudolasibolus minutissimus* Agerer which likewise has no cystidia and no clamp connections but differs in crystal-incrusted basal hairs and more cyphelloid shape, and clavate basidia. It depends on the weight one gives to these characters whether or not *Pseudolasibolus* can be included in *Cyphellostereum*. Since *Cyphellostereum* is mostly (although not constantly) muscigenous and *Pseudolasibolus* lignicolous I am more inclined to consider the latter as a separate genus.

*State of knowledge:* Only one species is completely known to the present author.

*Practical importance:* Unknown.

## SPECIES

*C. laeve* (Fr.) Reid (Cantharellus, Fr.; Cyphella, Lundell & Nannf.; Leptoglossum, W.B. Cooke; Stereophyllum boreale Karst.); possibly congeneric: *C. pusiolum* (Berk. & Curt.) Reid; *Leptoglossum seticolum* Corner (described without cystidia but according to Redhead with cystidia and identical with *C. laeve*). - *Pseudolasiobolus minutissimus* Agerer is possibly congeneric with *Stereum pusiolum* Berk. & Curt. (see discussion above).

### Tribus *Leucopaxilleae* Sing.

*Sydowia* 2: 29. 1948.

*Type genus: Leucopaxillus* Boursier.

*Characters:* Habit of the carpophores mostly clitocyboid or tricholomatoid, more rarely pleurotoid (but fleshy), collybioid, or omphaliod; spores constantly amyloid, ornamented or not; hyphae with or without clamp connections, without gelatinous layers, inamyloid; hymenophoral trama regular to almost subirregular (not bilateral); cystidia present or absent (macrocystidia none); true metuloids none; epicutis usually a cutis, more rarely somewhat trichodermial, but its hyphae not strongly differentiated (not acanthocystoid, without spherocysts or Rameales-structure, but sometimes with some dermatocystidia); veil none, or slightly developed. On the soil, on wood, rarely on grass roots, or various vegetable débris, on anthills, not ectomycorrhizal, or ectomycorrhizal (obligatorily so in some species of *Porpoloma*).

### KEY TO THE SUBTRIBUS AND GENERA

- A. Spores all smooth, with homogeneous, rarely heterogeneous (type XI) wall.
- B. Hyphae with clamp connections.
  - C. Habit tricholomatoid to more often clitocyboid, gigantic or at least large and fleshy; stipe at least 20 mm broad; cheilocystidia absent, or if present, not making the edge completely heteromorphous, rather small and inconspicuous; lamellae close to crowded; context neither yellowing nor reddening; spores small to medium (not over 8.3  $\mu\text{m}$  long); epicutis without distinct pigment incrusted. Growing on the ground (see "G" below).
  - C. Habit tricholomatoid, clitocyboid, omphaliod, collybioid, mycenoid, or pleurotoid; never gigantic; not combining the characteristics indicated above. On the ground as well as on wood, charcoal, etc.
    - D. Lamellae strongly, often repeatedly forked; habit clitocyboid; context and epicutis of soft, little coherent texture (KOH, NH<sub>4</sub>OH); spores often elongated; lamellae white, tending to pink; cheilocystidia none; epicutis without dark incrusting pigments. Growing on the ground, usually among mosses.
      - Subtribus *Porpolomatinae* (part)
      - 42. *Cantharellula*, p. 289

D. Lamellae sometimes forked but not strongly, never repeatedly so; habit clitocyboid or different; context not particularly soft; spores short or elongated; lamellae not tending to pink; cheilocystidia present or absent; incrusting pigment present or absent. Growing on the ground or lignicolous, sometimes on charcoal.

E. Habit tricholomatoid; growing on the ground, often ectomycorrhizal, or else with a strong odor or turning yellow or reddish or with heterogeneous spore wall.

47. *Porpoloma*, p. 294

E. Habit omphaloid, collybioid, mycenoid, pleurotoid, more rarely almost clitocyboid; never ectomycorrhizal; never with heterogeneous spore wall.

F. On earth, charcoal, or tussocks, not lignicolous; epicutis of pileus mostly not or only thinly pigment-incrusted, surface of pileus not radially fibrillose or rimose; lamellae rarely yellow, always decurrent; habit omphaloid; cheilocystidia often present but then filamentous and inconspicuous; odor often farinaceous; taste often unpleasant or bitter.

44. *Pseudoomphalina* p. 290

F. Mostly lignicolous species with different combination of characters.

G. Pileus yellowish with gray; pigments distinctly incrusting; lamellae yellow; habit of a large *Omphalina*.

43. *Pseudoarmillariella* p. 290

G. Pileus and stipe without yellow tinges; pigments not incrusting; habit omphaloid, mycenoid, collybioid or pleurotoid.

46. *Clitocybula*, p. 293

B. Hyphae without clamp connections. Subtribus *Porpolomatinae* (part) 45. *Pseudoclitocybe*, p. 291

A. Spores not smooth, but with amylaceous punctuation, verrucosity or spinules.

Subtribus *Leucopaxillinae*

48. *Leucopaxillus*, p. 296

49. *Melanoleuca*, p. 299

### Subtribus *Porpolomatinae* (Bon) Sing.\*

Spores smooth, with homogeneous, rarely slightly heterogeneous (type XI) wall.

Type genus: *Porpoloma* Sing.

Note: This subtribus represents a well circumscribed and easily identifiable group of genera. It has been stressed by Kühner that in some cases its affinities may be closer to genera outside the tribus Leucopaxilleae than to other genera within this tribus, but this is a matter of speculation rather than a matter of demonstrable affinities. Unless new and forceful data become known to prove that this subtribus is indeed an "artificial" one, we believe that it is perfectly valid, taxonomically sound, and a useful unit for the identifier. Additional anatomical and cytological studies are required for some, especially non-European species. But all American and tropical material studied by me has neatly fitted into the set of genera as outlined in the key and the following descriptions. As the question stands now, it depends on our general view on the importance of amyloidity of the spores versus habit (tricholomatoid versus clitocyboid) and whether amyloid spore walls are considered derived (from inamyloid ones) or primitive. I have repeatedly stated that it is dangerous to generalize on such assumptions. The number of nuclei per hyphal cell in the stipe, the number and size of oil drops in the strictly fresh spores, and modern chemical pigment analyses, quantity of urea formed etc., are possibly of some value - but far too few species of the world flora have been checked to be affirmative about this. Some of these characters are undoubtedly of some value in the establish-

\*st.n. (tr. *Porpolomataceae* Bon, *Docum. Mycol.* fasc. 12: 6. 1974.).

ment of affinities in certain groups of Agaricales, but whether they are useful for the classification of the subtribus *Porpolomatinae* is still very doubtful.

## 42. CANTHARELLULA Sing.

*Rev. Mycol.* 1: 281. 1936.

*Type species:* *Cantharellula umbonata* (Gmelin ex Fr.) Sing.

*Characters:* Habit of the carpophores clitocyboid; pigment dissolved in the cell sap and/or intraparietal; pileus fleshy, opaque to almost subtomentose, smooth, non-striate, convex to deeply infundibuliform; epicutis consisting of elongate ordinary hyphae, not cellular; lamellae deeply decurrent, close to distant, repeatedly forked, white or pink; spore print pure white; spores hyaline, smooth, distinctly amyloid, acyanophilic, cylindric or ellipsoid-oblong, never with both the inner and outer side convex nor the quotient of length and breadth smaller than 2; basidia normal but sometimes comparatively long, usually 4-spored; cheilocystidia absent or inconspicuous; cystidia otherwise not present; hymenophoral trama subirregular to almost intermixed, sometimes partly subgelatinous; subhymenium intermixed-subramose; stipe central, neither tubular nor truly cartilaginous but fleshy to fleshy-fibrous, solid to stuffed; veil none; context often reddening; clamp connections present; tissues becoming pale yellow (inamyloid) in Melzer's reagent. On the soil and among mosses.

*Development of the carpophores:* Gymnocalypous and stipitocarpous.

*Area:* Temperate zones.

*Limits:* This genus is easily separable from the related ones of the tribus by the combination of characters indicated above. Other species with strongly forked lamellae are those of *Cantharellus* (basidia stichic), *Hygrophoropsis* (spores short, cyanophilic), one form of a *Leucopaxillus* (spores short, asperulate), two species of *Clitocybe* (spores inamyloid), *Plicatura* (hymenium and hymenophore of the Meruliaceae-type, spores inamyloid, on wood), and *Geopetalum* (spores inamyloid; metuloids present, trama dimitic); there are also some occasional specimens in species of the Marasmieae that might have strongly forked, narrow lamellae, but they have an entirely different habit and could hardly be looked for in the *Leucopaxilleae* since they are delicate, small, white, mycenoid or omphalioid or "reduced".

*State of knowledge:* Two species completely known.

*Practical importance:* Edible according to Herrmann (*C. umbonata*).

## SPECIES

*C. umbonata* (Gmelin ex Fr.) Sing. [Merulius, Pers.; *Cantharellus*, Fr.; *Clitocybe*, Konrad; *Cantharellus muscoides* (Wulfen ex) Schröter; Chantarel muscoides

(Wulff ex) Murr.; *Cantharellus dichotomus* Peck] and forma *roseolamellata* Sing.; *C. infundibuliformis* Sing.; according to Horak (1971) also *C. waiporiensis* (Stevenson) Horak but described with incrusted pigment and probably rather *Pseudooomphalina*.

#### 43. PSEUDOARMILLARIELLA (Sing.) Sing.

*Mycologia* 48: 725. 1956.

*Type species: Cantharellula ectypoides* (Peck) Sing.

*Syn.: Cantharellula* subgen. *Pseudoarmillariella* Sing., *Sydotia* 2: 29. 1948.

*Characters:* Habit of the carpophores omphalioid, or more precisely of *Gerronema*; pigment incrusting; pileus opaque, appressedly fibrillose-subpunctulate in a radial arrangement, hygrophanous, with parallel or subparallel radially arranged hyphae making up the cuticle; context not reddening when bruised; clamp connections present; lamellae strongly decurrent and rather distinctly forked in most cases; hymenophoral trama subirregular, its hyphae interwoven; subhymenium subirregularly intermixed-subramose, its elements short, strongly interlaced-curved in all directions and therefore at times appearing cellular (much like the subhymenium of *Cantharellula*). On decaying and decayed wood.

*Development of the carpophores:* Unknown.

*Area:* North America.

*Limits:* This is closest to *Cantharellula* and *Gerronema*, differing from the former in the characters indicated in the key and from the latter in the amyloid spores which are somewhat elongated and the incrusting pigment.

*State of knowledge:* One species known.

*Practical importance:* Unknown.

#### SPECIES

*P. ectypoides* (Peck) Sing. (*Cantharellula*, Sing. 1942).

#### 44. PSEUDOOMPHALINA (Sing.) Sing.

*Mycologia* 48: 725. 1956.

*Type species: Omphalia kalchbrenneri* Bres.

*Syn.: Cantharellula* subgen. *Pseudoomphalina* Sing., *Sydotia* 2: 30. 1948.

*Characters:* Habit of the carpophores omphalioid (or like a small *Clitocybe*); pigment incrusting or not, macroscopically ochraceous, alutaceous or orange buff,

clay color, deep cinnamon, or perhaps umbrinous; pileus not quite opaque, glabrous, hygrophanous or almost so, non-fibrillose, the cuticle of the pileus consisting of subparallel to parallel hyphae which are radially arranged; context not reddening but sometimes colored almost as deeply as the surfaces when wet; hyphae of the carpophores with clamp connections, inamyloid; hymenophoral trama subregularly arranged (though a majority of its hyphae more or less axillarly directed) and often strongly interwoven, its elements strongly variable in shape and size; subhymenium irregular-ramose, of short curved elements and at times appearing cellular. On earth, humus and charcoal.

*Development of the carpophores:* Unknown.

*Area:* Temperate zone of the Northern hemisphere, and montane tropical forests of Northern South America.

*Limits:* This corresponds to *Omphalina* and *Gerronema* from which it differs in amyloid spores. Among the smooth-spored Leucopaxilleae, it is easy to separate from related groups by the habit and pigmentation, habitat and cuticle (of pileus) characters. There are no difficulties in delimitation.

*State of knowledge:* Seven species are rather completely known although one of them might belong here but has not been restudied by the author.

*Practical importance:* Unknown.

## SPECIES

*P. kalchbrenneri* (Bres.) Sing. (*Omphalia*, Bres.; *Xeromphalina*, Sing. 1942); *P. compressipes* (Peck) Sing. (*Clitocybe*, Sacc.); *P. graveolens* (Petersen) Sing.\*; *P. farinacea* (Murr.) Sing.\*\*; *P. felloides* (Kauffm.) Sing. [*Clitocybe*, Kauffm.; *Clitocybe fellea* var. *glareosa* Kauffm. sec. A.H. Smith; *Cantharellula felloides* (Kauffm.) Sing.]; *P. intermedia* (Kauffm.) Sing. sensu A.H. Smith (*Clitocybe*, Kauffm.; *Cantharellula*, Sing. 1951); *P. arsitophylli* Sing. - According to Bigelow also *A. apertus* Peck (*Clitocybe*, Sacc., Bigelow; *Clitocybula*, Sing.).

### 45. PSEUDOCLITOCYBE (Sing.) Sing.

*Mycologia* 48: 725. 1956.

*Type species:* *Cantharellula cyathiformis* (Bull. ex Fr.) Sing.

Syn.: *Cantharellula* subgen. *Pseudoclitocybe* Sing., *Ann. Mycol.* 41: 64. 1943.

*Omphalius* (Pers.) Roussel ex Earle, *Bull. N.Y. Bot. Gard.* 5: 432. 1909\*\*\*.

\*c.n. (*Omphalia graveolens* S. Petersen, *Danske Agaricaceer* 1: 1907.)

\*\*c.n. (*Clitocybe farinacea* Murr., *N. Am. Fl.* 9: 401. 1916.)

\*\*\*Whether *Omphalius* and *Omphalia*, although different in termination, must be regarded as variants of the same name in view of their common type species (or at least closely related type), according to the

**Characters:** Habit of the carpophores clitocyboid or clitocyboid-tricholomatoid; pigment either predominantly incrusting or predominantly intracellular, mostly fuscous or gray; pileus not quite opaque, glabrous or somewhat radially fibrillose even fibrillose squamulose at times, mostly ± hygrophanous, its cuticle consisting of somewhat subparallel hyphae which are radially arranged, much like those of *Tricholoma* subgen. *Tricholoma* but in some species hyphae ascending to form a trichodermium, or scattered cystidiod terminal cells; lamellae usually slightly and occasionally forked, usually more or less deeply decurrent but at times sinuate-broadly-adnate or irregularly attached, narrow to rather broad; context not reddening when bruised; clamp connections in the hyphae of the carpophores absent, hymenophoral trama rather regular, at least near edge, consisting of rather broad hyphae which are not incrusted by pigment toward the back of the lamellae, becoming rather irregular or interwoven in age; subhymenium cellular or subcellular. On earth and on foliage, also on wood débris and on decayed stumps and logs, needle beds, and other litter, also among deep moss, rarely on dung in shady places or on grass tussocks.

**Development of the carpophores:** Unknown.

**Area:** Temperate zone of Northern Hemisphere, one species in Southern Brazil, Paraguay, and Argentina.

**Limits:** This is close to *Porpoloma* from which it differs in more clitocyboid habit, and absence of clamp connections. It differs from *Armillariella* and *Tricholoma* in amyloid spores. It is not closely related to *Clitocybe*. Among the *Porpolomatinae*, it is unique because of the lack of clamp connections.

**State of knowledge:** We are able to indicate six species known well enough to be inserted here with certainty. These species are closely related to each other and should be studied monographically.

**Practical importance:** *P. cyathiformis* is edible but of small importance.

## SPECIES

*P. cyathiformis* (Bull. ex Fr. p.p.) Sing. (Clitocybe, Kummer; Cantharellula, Sing. 1936); *P. obbata* (Fr.) Sing. (Clitocybe, Quél.; Cantharellula, Bousset); *P. oregonensis* (Murr.) Sing. (Clitocybe, Murr., Cantharellula, Sing. 1942); *P. coprophila* (Speg.) Sing. (Clitocybe, Speg.; Cantharellula, Sing. 1951); *P. bacillaris* (Pers.) Sing. (Agaricus, Pers.); *P. martianis* Sing.; *P. beschidica* Sing. & Kuthan obviously also the *Clitocybe expallens* (Pers. ex Fr.) Kummer sensu Ricken, Kühner

Code Art. 75; as Donk believes (*Nova Hedwigia Beih.* 5: 204. 1962), is still somewhat doubtful. If they were not homonymous in this sense, *Pseudoclitocybe* would have to be considered a synonym of *Omphalia* and the species belonging here be transferred to *Omphalia*. The question to decide is whether *Russula* (adusta) and *P. cyathiformis* are sufficiently related and similar to warrant fear of confusion, or if a confusion might be likely for any other reason (since both appear to go back to a common pre-Friesian source). Those who cite *Omphalia* (Fr.) Staude non L. would add this here as a further synonym.

& Romagnesi, (non Bres., Sing.) if not conspecific with *P. cyathiformis*, and *P. atra* (Velen.) Harmaja (unless too close to *P. coprophila*).

#### 46. CLITOCYBULA (Sing.) Métrod

*Rev. de Mycologie* 17: 74. 1952.

*Type species: Fayodia lacerata* (Lasch) Sing.

*Syn.: Fayodia* subgen. *Clitocybula* Sing., *Ann. Mycol.* 41: 63. 1943.

*Cantharellula* subgen. *Neocantharellula* Sing., *Sydotia* 6: 194. 1952.

**Characters:** Habit typically of the smaller Clitocybes but varying to omphalioid, collybioid, mycenoid, and pleurotoid; cheilocystidia numerous or scattered, sometimes making the edge heteromorphous, in other species none; pleurocystidia sometimes present; dermatocystidia none or only dermatocystidioid hyphal ends present in center of pileus; spores varying from subglobose to ellipsoid-subcylindric, smooth, rarely faintly rounded-subangular in some spores; hyphae with clamp connections; pileus in the majority of the species somewhat lineate radially by innate fibrils, at times somewhat radially fibrillose-rough or even radially rimose; stipe and pileus thin-fleshy to thick-fleshy, the former often gregariously to cespitosely aggregate, early solid or narrowly stuffed, but in some soon becoming tubulose, in some almost cartilaginous, in others more fibrous-fleshy when old; subhymenium irregular-ramose although sometimes seemingly cellular; hymenophoral trama regular, its hyphae varying from subparallel to interwoven; pigments generally intracellular, varying according to species from melleous to gray, fuliginous, or blue. On rotting and buried twigs, logs, trunks, etc. in the forest.

**Development of the carpophores:** Unknown.

**Area:** Temperate zones of the Northern and Southern Hemispheres; two (bright colored) species in the neotropics.

**Limits:** This genus has sometimes the appearance of *Gerronema* but differs clearly in amyloid spores; it differs from *Pseudoarmillariella* in scarce or wanting incrusting pigment and scarce or wanting yellow pigments, also in somewhat more regular hymenophoral trama, and in always much less elongated spores. In the omphalioid as well as also the pleurotoid species, cheilocystidia are often present and even pleurocystidia are found in some species. The - thus far strictly South American - pleurotoid section of the genus has much fleshier pileus and stipe than *Panellus*; the epicutis-hyphae of the pleurotoid section are sometimes vaguely incrusted as they are in some Porpolomas from which they differ in the pleurotoid habit with decurrent lamellae and the lignicolous habitat.

It must also be noted that some of the species with smaller carpophores observed in *Clitocybula* may be superficially similar to *Hydropus* (Myceneae), section *Floccipedes* subsection *Spuriae*, but have distinctly more affinity with *Clitocybula* than with the typical *Hydropus*-species. The latter can be distinguished from *Clitocybula* by the particularly narrow and sometimes pigmented hyphae which

form the very shallow layer of the cutis-like epicutis which is sharply differentiated from the hypodermium; besides, these species of *Hydropus* have either very large pleurocystidia or gelatinized hymenopodium or epicutis - features absent in *Clitocybula*. If dermatocystidia are present in *Clitocybula*, they are restricted to the center of the pileus.

*State of knowledge:* Nine species are here recognized.

*Practical importance:* Unknown.

## SPECIES

Subgenus I. **Clitocybula**. Cheilocystidia either absent or scattered to numerous, but mostly not making the edges of the lamellae heteromorphous; pleurocystidia present or absent; stipe central or nearly so. Northern Hemisphere and tropics.

*Type species:* *C. lacerata* (Scop. ex Lasch) Métrod.

*C. familia* (Peck) Sing.; *C. lacerata* (Scop. ex Lasch) Métrod; *C. oculus* (Peck) Sing.; *C. tilieti* (Sing.) Sing.; *C. abundans* (Peck) Sing.; *C. azurea* Sing.; *C. cyancephala* (Pat.) Sing. (Collybia, Pat.).

Subgenus **Neocantharellula** (Sing.) Sing. Cheilocystidia numerous (but moderately voluminous), making the edge of the lamellae heteromorphous, but often easily collapsing (as in *Porpopoma*); pleurocystidia none; habit between pleurotoid and clitocyboid, i.e. fleshy fungi with eccentric stipe and decurrent lamellae; spores never subglobose. Species of the Southern Hemisphere, temperate.

*Type species:* *C. tarnensis* (Speg.) Sing. sensu Sing. 1951 (11-II-1950, M185).

*C. tarnensis* (Speg.) Sing. at least sensu Sing.; *C. mellea* Sing.

## 47. PORPOLOMA Sing.

*Sydotia* 6: 198. 1952.

*Type species:* *Porpoloma sejunctum* Sing.

*Characters:* Habit tricholomatoid; pileus dry, innately fibrillose, or with a superficial fibrillosity or granular-fibrillose, or with squamules and tomentum; often rimose; intraparietal pigment often present and then incrusting the walls of the cuticular hyphae; clamp connections present; lamellae sinuate to emarginate or adnate or adnate with a decurrent tooth; spores with homogenous or weakly heterogenous wall which in the latter case shows weakly cyanophilous insertions, otherwise acyanophilous, amyloid, smooth (the young spores are always provided with a smooth, homogenous, acyanophilous wall); spore print pure white; hymenophoral trama regular; subhymenium consisting of subisodiametric to elongated small elements; stipe never eccentric, fleshy; context in some species reddening or yellowing; cheilocystidia present, more rarely absent, often making the

edge of the lamellae distinctly heteromorphous. On forest humus and earth in shaded places and outside the woods in parks and grasslands.

*Development of the carpophores:* Unknown.

*Area:* In temperate zones of the Northern as well as Southern hemisphere (in the southern Hemisphere in the *Nothofagus*-zone, rarely in the tropics).

*Limits:* Some of the species remind one of certain groups of *Tricholoma* from which they strongly differ in the combination of hyphae with clamp connections, amyloid spores, and heteromorphous gill edge. Others remind one of *Hygrocybe* section *Tristes* from which they differ in shorter basidia and amyloid spores. The apparent thickness of the lamellae is due to the broader hymenophoral trama. The only amyloid-spored hygrophoraceous fungus known is *Neohygrophorus angelesianus* which has basidia decidedly >5 times longer than the long axis of the spores, and which looks much more like a *Camarophyllus* than a *Hygrocybe*; it also has the strongly interwoven and relatively narrow hyphae of the hymenophoral trama characteristic for *Camarophyllus* rather than the broad and strictly regularly arranged hyphae characteristic for *Porpoloma*. The smooth-spored species of *Leucopaxillus* differ from *Porpoloma* in the characters indicated in the key. Those species of *Porpoloma* which have heterogeneous spore wall differ from *Fayodia* in totally different habit, the young acyanophilous spores and the hygrophanous pileus aside from the different cystidial characters.

*State of knowledge:* Eight species belong here.

*Practical importance:* The species of the Southern Hemisphere are obligatorily ectomycorrhizal with *Nothofagus* and therefore important in forestry.

## SPECIES

Subgenus **Pogonoloma** Sing. (1961). Margin of pileus pilose; odor of *Inocybe bongardii*, or hyacinths. Pigment intracellular. Cheilocystidia poorly differentiated or none. Not ectomycorrhizal.

Type and only species: *P. spinulosum* (Kühner & Romagnesi) Sing.

Subgenus **Pseudotricholoma** (Sing.) Sing. Pileus surface not pilose but granular, fibrillose-tomentose, often rimose or subglabrous; odor farinaceous or of cucumber. Pigments intraparietal, often incrusting; cheilocystidia present or absent; apparently not ectomycorrhizal(?).

Type species: *Tricholoma umbrosum* A.H. Smith & Walters.

*P. metapodium* (Fr. ex Fr.) Sing. (*Hygrophorus*, Fr. ex Fr.) and what appears to be a form or geographical race of it: *P. umbrosum* (A.H. Smith & Walters) Sing.; *P. elytroides* (Fr.) Sing. (sensu Romagnesi; Fries, Epicr. p. 39. 1838 as *Agaricus*; Romagnesi, Bull. Soc. Myc. Fr. 65: 132. 1949); *P. pescaprae* (Fr.) Sing.

**Subgenus Porpoloma.** Margin of pileus not pilose; odor none. Pigment intracellular and/or intraparietal; cheilocystidia numerous, making the edge of the lamellae heteromorphous; obligatorily ectomycorrhizal with *Nothofagus* and apparently other Fagales.

*Type species:* *P. sejunctum* Sing.

*P. sejunctum* Sing.; *P. portentosum* Sing.; *P. terreum* Sing.; apparently also *P. amyloideum* (Stevenson) Horak and *P. boninense* (S. Ito & Imai) Hongo.

Subtribus *Leucopaxillinae* Sing.

subtrib. nov.\*

Spores with amylaceous punctuation, isolated or partially connected warts or spinules on much less amyloid or inamyloid ground; if smooth - carpophores gigantic or large and fleshy.

*Type genus:* *Leucopaxillus* Bours.

#### 48. LEUCOPAXILLUS Boursier

*Bull. Soc. Myc. Fr.* 41: 391. 1925; em. Singer, *Rev. Mycol.* 4: 69. 1939.

*Type species:* *L. pseudoacerbus* (Cost. & Duf.) Boursier [= *L. tricolor* (Peck) Kühner].

*Syn.:* *Aspropaxillus* Kühner & Maire. *Bull. Soc. Mycol. Fr.* 50: 13. 1934.

**Characters:** Habit of the carpophores clitocyboid, tricholomatoid, or very rarely somewhat pleurotoid: pileus opaque, non-hygrophanous, rarely with hygrophanous spots, not viscid, with smooth or short-ribbed to crenate, initially involute margin, thick, fleshy but not watery; cuticle little differentiated; lamellae decurrent, or sinuate, or emarginate-sinuate, or adnexed to adnate; often developing cyanic acid (sect. I); spore print pure white; spores (Pl. 68A) hyaline, rough to warty without a distinct suprahilar plage, or smooth, and then usually slightly (even inconstantly) amyloid (but the species with warty spores strongly amyloid because of the exosprium causing the ornamentation above an otherwise smooth wall), the ornamentations cyanophilous, spores rather small to medium sized (up to 10 µm long), rather short-ellipsoid, subglobose, ovoid; basidia normal sometimes some scerified and pseudoamyloid (in *L. patagonicus*); cystidia none; cheilocystidia, however, sometimes differentiated but small and not very conspicuous; hymenophoral trama regular to subirregular (more irregular in age); subhymenium ramosc (filamentous), thin; stipe central, very rarely eccentric, usually thick and fleshy to somewhat tough; veil none; pigment intracellular, or incrusting in the cuticle of certain species (Pl. 63, A7), macroscopically often bright colored, in

\*Sporis amylaceo-ornamentatis vel raro levibus.

some species wanting; context unchanging on bruising; its hyphae inamyloid and with numerous clamp connections (but said to be clampless in some form of *L. mirabilis* which this author considered as belonging to *Melanoleuca* but Moser declared inseparable from *L. mirabilis*). On humus and débris, especially foliage, needle beds, even anthills.

*Development of the carpophores:* Gymnocalypous ("decidedly gymnocarpous" in *L. cerealis* according to Kühner).

*Area:* Boreal to subtropical zones in the Northern as well as in the Southern Hemisphere.

*Limits:* Since all characters excepting the strongly amyloid (or rather amylaceous) exosporium are identical in section *Aspropaxilli* and in *Eu-Leucopaxilli*, Singer (1939) and Singer & Smith (1943) have not followed Kühner & Maire who separated the species without ornamentation from the main genus *Leucopaxillus* as an autonomous genus. We are equally opposed to a recombination of *Aspropaxillus* with *Clitocybe* and *Tricholoma* since a rejection of spore amyloidity as a generic character on principle is just as artificial as its adoption on that level in all cases (see also under *Clitocybe*, p. 240). Métrod (1939) has combined the genera *Leucopaxillus* and *Melanoleuca* under the common name *Melanoleuca*, claiming that there are no constant differences between the two genera. The author disagrees with Métrod's observations. The genus *Melanoleuca* is constantly different from *Leucopaxillus* in the absence of clamp connections which are plentiful in *Leucopaxillus*. The plage on the spores of *Melanoleuca* is almost as good a character but not always easy to demonstrate, especially in those species that have a very slightly developed ornamentation.

On the other hand Bigelow & Rowley (*Mycologia* 60: 874. Fig. 3. 1968) observed a plage on surface replicas SEM although the plage area sometimes had (amyloid?) processes in the form investigated viz. *L. albissimus* var. *lentus* (recte *L. cerealis* var. *lentus*). Whether this type of plage is comparable with the one observed under the light microscope in the *Melanoleucas* is not fully clear, but undoubtedly these observations tend to diminish the value of the plage as a decisive generic character in the delimitation of *Melanoleuca* vs. *Leucopaxillus*. The inconstancy of the leptocystidia in *Melanoleuca* has been indicated before by Heim and Singer, but Josserand has added a new character distinguishing the two genera, viz. the angular shape of the spores of *Melanoleuca* when seen from one end (in vertical position) after chemical removal of the interstratum. Kühner has shown that there is a pigment formation in *Melanoleuca* that does not occur in *Leucopaxillus*.

There are no other problems in the delimitation of *Leucopaxillus* which is a remarkably well defined and very homogeneous genus.

*State of knowledge:* The genus has been monographed, and the knowledge of the species is nearly complete. In their monograph, Singer & Smith distinguished 18 species and varieties; in addition, 1 variety and 7 new species have been discovered since then, which brings the number of autonomous species up to 19.

*Practical importance:* *Leucopaxillus giganteus* and *L. candidus* have been mentioned in some European papers as a new source of an antibiotic substance named "clitocybine" with a potential application against tuberculosis. - The investigations by Moser (1963) and Marx (1969) have shown that at least some species of *Leucopaxillus* are (facultative?) ectotroph-formers, and thus of some potential importance in forestry; these species produce a particularly abundant and efficient antibiotic. According to Marx, the substances with bacteriostatic properties contained in *L. cerealis* var. *piceinus* are

- (1) HOOC-CH=CH-C≡C-C≡C-C≡N, and  
(2) HOOC-CH=CH-C≡C-C≡C-CO-NH<sub>2</sub>.

The mycelium of *L. giganteus* may cause "a 40-100 m broad necrotic zone where the entire green vegetation dies" (Kreisel). Furthermore, *L. lepistoides* and some other species are edible.

## SPECIES

Sect. 1. *ASPROPAXILLI* (Kühner & Maire) Sing. & Sm. (1943). Spores smooth, slightly amyloid (Pl. 63, A3).

Type species: *L. giganteus* (Fr.) Sing.

*L. candidus* (Bres.) Sing. (Clitocybe, Bres.); *L. giganteus* (Fr.) Sing. (Clitocybe, Quél.; Paxillus, Fr.; Aspropaxillus, Kühner & Maire; Melanoleuca oreades Murr.); *L. sainii* Sing. ined. (with cheilocystidia); *L. septentrionalis* Sing. & Sm.; *L. lepistoides* (Maire) Sing. (Tricholoma, Maire; Aspropaxillus, Kühner & Maire); probably also *L. macrocephalus* (Schulz.) Bohus\*.

Sect. 2. *LEUCOPAXILLUS* (*Typici* Sing. 1943; *Eu-Leucopaxilli* Sing. & Sm. 1943). Spores rough from a warty exosporium which is very strongly amyloid (Pl. 63A, 1-2, 4-6).

Type species: *L. pseudoacerbus* (Cost. & Duf.) Boursier.

*L. cerealis* (Lasch) Sing. [Agaricus, Lasch; Clitocybe albissima (Peck) Sacc.; Leucopaxillus, Sing.; Clitocybe subhirta (Peck) Peck; Tricholoma lendum (Post apud Romell) Sacc.; Lepista barbara Maire; Clitocybe paradoxa Cost. & Duf.; Clitocybe albiformis Murr.; Clitocybe stipitata Murr., these synonyms belong to the type variety and eight other varieties of this species]; *L. nauseosodulcis* (Karst.) Sing. & Sm. (Clitocybe, Karst.; Pleurotus, Sacc.); *L. subzonalis* (Peck) Bigelow (L. pulcherimus (Peck) Sing. & Sm.; Clitocybe, Peck); *L. rickii* Sing.; *L. patagonicus* Sing.; *L. laterarius* (Peck) Sing. & Sm. (Tricholoma, Sacc.); *L. rhodoleucus* (Romell) Kühner (Clitocybe, Sacc.); *L. tricolor* (Peck) Kühner (Tricholoma pseudoacerbum Cost. & Duf.; Leucopaxillus, Boursier); *L. brasiliensis* (Rick) Sing. & Sm.; *L. mirabilis* (Bres.) Kühn. in Kühn. & Romagnesi (Tricholoma, Bres.); *L. gentianaeus* (Quél.)

\*Unknown to me; may be rather *Porpoloma*, subg. *Pogonoloma* (?) cf. Bon, *Docum. Mycol.* 9(33): 26-28. 1978.

Kotlaba (*L. amarus* (A. & S. ex Fr.) sensu Kühner; *Clitocybe vulpecula* (Kalchbr.) Sacc.; *Melanoleuca bicolor* Murr.; *Melanoleuca roseibrunnea* Murr.] with several forms and varieties); *L. gracillimus* Sing. & Sm. with var. *rappii* (Murr.) Sing. (*Clitocybe rappii* Murr.); *L. alboalutaceus* (Møller) Møller (if specifically different from *L. gentianeus*) which seems hardly different from *L. baeospermus* Kühn. in Kühn. & Romagnesi.

#### 49. MELANOLEUCA Pat.

*Cat. rais. Pl. cell. Tunisie*, p. 22. 1897.

*Type species: Melanoleuca vulgaris* Pat.

*Syn.: Melaleuca* Pat., *Hymen. Eur.*, p. 96. 1887 (non Linné 1767).

*Characters:* Habit tricholomatoid, more rarely collybioid-tricholomatoid or clitocyboid; pigment dusky or pale gray, fuscous, umber, etc. more rarely yellowish-ocher, or absent; pileus glabrous, or pruinose, or innately fibrillose, most frequently perfectly glabrous, hygrophanous or non-hygrophanous, epicutis little differentiated, consisting of interwoven, repent, elongate hyphae that are not radially arranged; lamellae white, or cream colored, or grayish, usually close to crowded, emarginate to decurrent; spore print pure white to cream color (A to C of Crawshay); spores hyaline, subsMOOTH to (mostly) warty from a strongly amyloid exosprium (after the chemical removal of the exosprium the subangular shape of the spores is revealed when they are seen from one end) on a very slightly amyloid main wall, with a more or less distinct plage on the inner side of the spores, the warts forming an ornamentation of the type IIIb, IV, IV-II, V, or VI, the outline of the spores ellipsoid-oblong, ellipsoid, more rarely short ellipsoid, the warts moderately high; basidia typically with siderophilous granulation of the micro-type and rather short, 4-spored; leptocystidia or cystidioles (Pl. 21, 5), often pseudocystidiod with characteristic apical crystals, or metuloid, usually present, very few species, and many individuals in certain species, devoid of cystidia; similar cystidia often as dermatocystidia on pileus and/or stipe; hymenophoral trama regular or almost so, with a slightly interwoven mediostratum, especially near the back of the lamellae; subhymenium cellular-subintermixed; stipe evelate, or much more rarely with an indistinct to distinct but rather incomplete annulus, usually central (very rarely eccentric), rather fibrous-fleshy in consistency and not truly cartilaginous or tough; context white, or, starting from the base of the stipe, becoming gray, brown, or almost black (from an intercellular-epicellular brown pigment characteristic for the genus), or colored so from the beginning; all hyphae without clamp connections. On the earth, in woods, and outside of the woods, often on manured pastures, in gardens, cold frames, greenhouses, also in prairies and steppes, even in semi-desert formations, also in the subalpine and alpine region and south to the tropical forests.

*Development of the carpophores:* Gymnocalypous, stipitocarpous (Watling 1985).

**Area:** Cosmopolitan but rare in the lowland tropics and Antarctica; most common in the temperate and frigid zones of both hemispheres.

**Limits:** The delimitation of *Melanoleuca* is by no means difficult in spite of the fact that what has been claimed as the main characters of the genus, viz. the cystidia and the verrucose spores are by no means constant. What is constant is the lack of clamp connections in the carpophore hyphae and the amyloid spores, the absence of incrusting or intraparietal pigment in the cuticular layer of the pileus (but it may be present in the stipe!). The cystidia are missing in some otherwise quite typical species, and the spores may be merely finely punctate or marbled, perhaps even absolutely smooth and their plage indistinct. Moser has apparently found a clamp-less form of *L. mirabilis* - not the clamp-less "variety" *nigrescens* Bres. (which is a *Melanoleuca*) - but occasional parthenogenetic forms might exist in many generally clamp-bearing (and not clamp-bearing) genera; such forms would still be easily recognizable as *Leucopaxillus* by the presence of intraparietal pigment in the cuticular layer of the pileus and the warty spores without plage, the different cystidia and dermatocystidia.

**State of knowledge:** Since the genus had been revised by Singer (1935) and later by Métrod, the precise ornamentation type and the development of the plage of the spores as well as the presence or absence of dermatocystidia on pileus and stipe, their shape and distribution, and also the exact color of the fresh spore print has been emphasized, and consequently, the data available for a number of species are insufficient, and the subdivision of the genus into sections or series should be reconsidered and modernized. A partial attempt to do so was published by Singer & Cléménçon (1972) and by Bon, *Docum. Myc.* 9(33): 37-43. 1978. At present it is only possible to enumerate the species and their groupings according to the usual classification, with the exception of a few species which are now completely known, and have been inserted in the section where they belong according to my former infrageneric taxa. Below, 48 species are enumerated. See also Pegler & Young (1978) and Bresinsky & Stangl (1977).

**Practical importance:** As far as it is known now, the main practical importance of the genus *Melanoleuca* consists in the edibility of the carpophores of virtually all series. The most valuable edible mushrooms of this genus are *M. evenosa* and *M. alboflavida* (both, however, very little used).

## SPECIES

Sect. 1. *ALBOFLAVIDAE* Sing. (1935 ut series, 1943). Pileus practically devoid of pigment, predominantly white, or bleaching to white, or ochraceous rather than grayish, or brownish; spore print (if pileus ochraceous) cream color, or, in other species, pure white; lamellae more often narrow than broad (narrow, in *Melanoleuca*, always means that the breadth of the lamellae is less than one tenth of the diameter of the pileus); spores either distinctly warty, or subsMOOTH.

*Type species: M. alboflavida* (Peck) Murr.

*M. evenosa* (Sacc.) Konrad (Tricholoma cnista ssp. evenosum Sacc.\*); *M. strictipes* (Karst. sensu Lundell) Métrod (Tricholoma, Karst.); *M. alboflavida* (Peck) Murr. (Collybia sedula Graff); *M. kavinae* (Pilát & Vesely) Sing.; *M. kalchbrenneri* Sing. (Agaricus dehiscens Kalchbr. non Viviani; Collybia, Sacc.; Melanoleuca, Sing.); *M. balansae* (Speg.) Sing. (Clitocybe, Sacc.); probably also *M. candida* (Vel.) Sing., *Clitocybe nobilis* Peck, and *M. tropicalis* Pegler.

Sect. 2. *HUMILES* Sing. (series, 1935; sect. 1943). Pileus well colored (gray, avellaneous-fuscous, fuscous, blackish), or soon becoming so; spore wall always distinctly warty from the well developed exosporium; stipe furfuraceous pubescent, or squamulose with black fibrils, or with an indistinct annulus; not entirely brown inside.

*Type species: M. humilis* (Pers. ex Fr.) Pat.

*M. verrucipes* (Fr. apud Quél.) Sing [Armillaria, Quél.; Tricholoma, Bres.; Clitocybe puellula (Karst.) Karst.]; *M. humilis* (Pers. ex Fr.) Pat. (Tricholoma, Quél.); *M. umbrinella* (Speg.) Sing. (Tricholoma, Speg.); here perhaps also an acystidiate species of *Melanoleuca* (perhaps *Tricholoma mirabile* var. *nigrescens* Bres.; *Icon. Mycol.*, pl. 92. 1927) which Bresadola confused with *Leucopaxillus mirabilis* (Bres.) Kühn. in Kühn. & Romagnesi.

Sect. 3. *OREINAE* Sing. (series 1935; sect. 1943). Pileus and spores as in sect. 2; stipe usually merely pruinose at the apex, and if wholly pruinose, the interior of the stipe is entirely brown; small carpophores with white or gray stipe and white or gray lamellae; if the diameter of the pileus is larger than 30 mm and the stipe is not thin as in the genus *Collybia*, the lamellae are always white and narrow and the stipe is usually pallid. (Very large species do not enter this section.)

*Type species: M. oreina* (Fr.) Kühner & Maire.

*M. catalaunica* Sing.; *M. oreina* (Fr.) Kühner & Maire (Tricholoma, Gillet); *M. graminicola* (Vel.) Kühner & Maire (Tricholoma, Vel.); *M. microcephala* (Karst.) Sing. (Tricholoma Karst.); *M. brevispora* Sing.; *M. paedida* (Fr.) Kühner & Maire (Tricholoma, Quél.); *M. excissa* (Fr.) Sing. (Tricholoma, Quél.); *M. spegazzinii* (Sacc. & D. Sacc.) Sing. [Tricholoma, Sacc. & D. Sacc.; Tricholoma humile Speg. non (Fr.) Quél.]; *M. tucumanensis* Sing.; probably also in this section: *M. subcinereiformis* Murr.; *M. cinerascens* Reid; *M. testata* (Britz.) Sing.; *M. rasilis* (Fr. sensu Bres.) Sing.; also a species which may be partly *Tricholoma strictipes* Karst. (as such determined by the author once); perhaps *M. deserticola* (Speg.) Sing. (Tricholoma panaeolum var. *deserticola* Speg.).

Sect. 4. *MELANOLEUCA* (*Vulgares* Sing. 1943). Pileus, spores, and surface of the stipe as in the preceding section; however, small species, unless the context is brown to a large extent, with a diameter of the pileus of 30 mm or less, and collybioid stipe,

\*According to Stangl & Bresinsky *A. indepressus* Britz. and *A. subalpinus* Britz. are identical; both would have priority over *M. evenosa*. Although their identity is very probable, the colors and spore measurements would have to be assumed as being erroneous and type specimens do not exist.

are here excluded, and go to sect. *Oreinae*; the larger species have either colored stipe or broad (more than one tenth of the diameter of the pileus) lamellae.

*Type species: M. vulgaris* Pat.

*M. grammopodia* (Bull. ex Fr.) Pat. (Tricholoma, Quél.); *M. longispora* Sing.; *M. subbrevipes* Métrod (M. bresadolae Sing.); *M. cognata* (Fr.) Konr. & Maubl. (Tricholoma, Gillet) and its subspecies (geographic race) ssp. *altaica* Sing.; *M. crassotunicata* Sing.; *M. turrita* (Fr.) Sing. (Tricholoma, Sacc.); *M. polioleuca* (Fr.) Kühner & Maire (Melanoleuca vulgaris var. polioleuca Konr. & Maubl.); *M. brevipes* (Bull. ex Fr.) Pat. (Tricholoma, Kummer); *M. melaleuca* (Pers. ex Fr.) Murr. [Tricholoma, Kummer; Melaleuca vulgaris Pat.; Melanoleuca vulgaris (Pat.) Pat.]; *M. adstringens* (Pers. ex Pers.) Métrod; *M. planiceps* (Peck) Sing. (Tricholoma, Peck); *M. stridula* (Fr.) Sing. (Collybia, Quél.); *M. arcuata* (Fr.) Sing. (Tricholoma, Quél. sensu Ricken; Tricholoma friesii Bres.); *M. reai* Sing.; *M. luteolosperma* (Britz.) Sing. (Tricholoma, Sacc.); *M. subpulverulenta* (Pers. ex Fr.) Sing. (Tricholoma, Karst.); *M. orientalis* (Pat.) Sing. (Collybia, Pat.); *M. melanosarx* Sing.; probably also in this section: *M. earlei* (Murr.) Sing.; *M. praecox* Murr.; *M. montana* (Britz.) Sing.; *M. amica* (Fr. sensu Bres.) Sing.; *M. phajopodia* (Bull. ex Fr.) Sing.; *M. griseofumosa* (Secr.) Sing. & Clément; *M. lixivia* (Fr. sensu) Maire; *M. sparrei* Sing.

*Note:* I hesitate to propose, under the present circumstances, a separate section for those species whose spore print has been found to be of a cream tinge when quite fresh; they seem to form a heterogenous group: *M. reai* Sing., *M. griseofumosa* (Secr.) Sing. & Clém.; *M. luteolosperma* (Britz.) Sing. and a similar form with other cystidial characters described by me from Patagonia; *M. alboflavida* (Peck) Murr. and several others.

### Tribus *Biannulariaeae* Sing.

*Ann. Mycol.* 34: 330, 347. 1936.

*Type genus: Biannularia* G. Beck (= *Catahelasma* Lovej.).

*Syn.: Armillarieae* Imai, *Journ. Fac. Agr. Hokkaido Imp. Univ.* 43: 46. 1938 (spec. & diagn. exclus).

*Characters:* Lamellae decurrent or adnate to sinuate-adnexed, inserted or with very few lamellulae; hymenophoral trama bilateral in young specimens often early becoming regular\*, inamyloid: spores oblong and large, or short-ellipsoid to ellipsoid and medium sized, always amyloid, smooth, with thin acyanophilic wall, uninucleate or binucleate; stipe fleshy; veil present, rather distinctly double in most species, but no basal volva present.

\*The hymenophoral trama consists in young specimens of a bilateral structure approximately of the *Phylloporus*-type, soon developing a mediostratum with broad  $\pm$  interwoven hyphae and with close septa (6-20  $\mu\text{m}$  broad), flanked by a lateral stratum of thinner hyphae, these often only 3-5  $\mu\text{m}$  broad, soon becoming regularly arranged in the layer near the mediostratum so that an intermediate *Clitocybe*-type structure is achieved, at maturity mostly completely regular, of less diameter than the mediostratum (each side about one third of the diameter of the mediostratum in *A. luteovirens*).

## KEY TO THE GENERA

- A. Lamellae distinctly decurrent; veil very distinctly double; spores very long ( $>9\ \mu\text{m}$ ), predominantly uninucleate 50. *Cataethelasma*, p. 303
- A. Lamellae adnexed to adnate, often sinuate, occasionally emarginate-subfree; veil present not consisting of an apical annulus and an annulus inferus but mostly distinctly double; spores not remarkably long, predominantly binucleate 51. *Armillaria*, p. 303

### 50. CATAHELASMA Lovej.

*Bot. Gaz.* 50: 383. 1910.

*Type species:* *C. evanescens* Lovej.

*Syn.:* *Biannularia* G. Beck, *Pilz- und Kräuterfr.* 5: 231. 1922.

*Characters:* Those of the tribus; lamellae decurrent; spores oblong (ellipsoid-oblong, ellipsoid-cylindric), predominantly uni-nucleate; veil distinctly double. On the soil in coniferous woods.

*Development of the carpophores:* Bivelangiocarpous.

*Area:* Europe and North America, and Japan, boreal in character.

*Limits:* Clearly separated from all other genera but evidently closest to *Armillaria* which differs in the characters indicated in the key. *Amanita* which has the same spores (amyloid and elongate in many species), bilateral trama (but of a different type of bilaterality), and double veil (though the vola usually distinctly basal) differs in the free lamellae, and, according to Kühner's data, in binucleate spores (uninucleate in *Cataethelasma*).

*State of knowledge:* Three of the (probably) five species have been studied thoroughly.

*Practical importance:* The well-known species are good edible mushrooms. They appear to be ectomycorrhizal with conifers.

## SPECIES

*C. imperiale* (Fr. apud Lund) Sing. (*Armillaria*, Quél.; *Armillariella*, Konr. & Maubl.; *Biannularia*, G. Beck; *Armillaria nobilis* Murr.); *C. ventricosum* (Peck) Sing. (*Lentinus*, Peck; *Armillaria*, Peck); *C. singeri* Mitchel & Smith; evidently also *C. evanescens* Lovej., and most probably *Armillaria macrospora* Peck.

### 51. ARMILLARIA Kummer

*Führ. Pilzk.*, p. 25. 1871; em. Sing., *Ann. Mycol.* 34: 331. 1936.

*Type species:* *A. straminea* (Krlz.) Kummer.

**Characters:** Those of the tribus; lamellae adnexed, even emarginate-subfree or sinuate, never decurrent; spores ellipsoid to short-ellipsoid. On the soil in frondose and coniferous woods.

**Development of the carpophores:** Monovelangiocarpous and stipiticarpous according to Reijnders in "*A. luteovirens*" (pers. comm.).

**Area:** Circumpolar.

**Limits:** The strongly developed veil, the binucleate spores, and, to a degree, structure of the trama and the subhymenium separate this genus clearly from the genera of the *Leucopaxilleae*, especially *Porpoloma*; the presence of a veil, the structure of the trama and the subhymenium, and the less broadly attached lamellae as well as the comparatively shorter basidia separate *Armillaria* from *Neohyphorus*; the non-decurrent lamellae, the absence of two annuli and the mostly smaller, typically predominantly binucleate spores separate *Armillaria* from *Catathelasma*.

This genus *Armillaria* was one of the most notoriously artificial genera of the Agaricales in the older classification. It was finally dismembered by Singer (*Rev. Mycol.* 5: 10. 1940). The species of *Armillaria* in the sense of Fries and Quélet are now distributed among the following genera: *Armillaria* sensu stricto, *Tricholoma*, *Calocybe*, *Armillariella*, *Melanoleuca*, *Leucocortinarius*, *Pleurotus*, *Catathelasma*, and *Oudemansiella*.

*Armillaria luteovirens* has somewhat the aspect of an *Amanita*, but the type and

\*Those who cite *Armillaria* (Fr.) Staude (which I consider inadmissible, see Art. 34.1, 35.4 and *Mycologia* 47: 270-272. 1955), with *A. mellea* as type species, would have to use Pouzar's generic name for the genus treated here unless the latter is transferred to *Porpoloma* Sing. (1952) as suggested by Kühner (1980) in spite of the conspicuous veil. Kühner gives as reason for his preference of *A. melleus* as type species the fact that in his taxonomy the Friesian tribus *Armillaria* would disappear. This is not an admissible reason. The reason for our choice of type species is mainly the fact that Kummer as he states himself, created new genera defining them like Fries defined his tribus but where he did so he certainly never took *Systema I* as his model and neither do we as far as his genera are concerned. Already in *Epicrisis* (p. 21, 1838) Fries describes *A. stramineus* from his own observation quoting "Krombh. t 25 f. 8-14". Even for *Armillaria* Fries the choice of *A. melleus* is not at all easily justified. Undoubtedly, aside from Karsten, Patouillard (1887) narrowed *Armillaria* down to two ("Ar. caligata, Ar. robusta ..."), species which means that he was indirectly selecting a type (*A. robustus*, see Fries, *Syst.* 1: 26. 1821) which was many years before Clements & Shear selected *A. melleus*. If all these facts are considered, Donk's remark (1962) ("If indeed Singer is correct... of course, his last choice has to be respected.") becomes meaningful.

Even those authors who, for some reason, feel obliged to cite *Armillaria* (Fr.) Staude should not follow Watling who insists on *A. melleus* as type species for that genus. While it is true that Clements & Shear chose this species as type species and were the first authors to do so, it is equally true that Fries in his synonymy of 1821 which defines the basic scope of the tribus, indicates "Batt. l.c. Lepiotae spec. Pers. l.c." Battara calls species attributable to the first three groups of *Armillaria* - *Lepiota*, joining them with other annulate species mainly of *Lepiota* sensu lato, but *A. melleus*, in Battara, enters "Polymyces Batt. p. 33" (so cited by Fries himself and later validated by Earle). Thus, the choice of *A. melleus* as type of *Armillaria* Fr. is therefore not in agreement with the protologue and should be rejected according to Art. 10.2, 7.13, 8.1, T. 4e of the 1983 Code.

degree of bilaterality, especially its development and hyphal structure, is different from that of the Amanitaceae sensu stricto, and the affinity of the genus *Armillaria* is rather with *Catathelasma* than with *Amanita*. All other Tricholomataceae with bilateral trama have mycenoid, collybioid or omphalioid habit, or else pink spores, and the anatomy of the covering layers of the pileus is quite different.

*State of knowledge:* The three species admitted here are completely known.

*Practical importance:* *A. luteovirens* is said to be delicious food (E. Hermann).

## SPECIES

*A. subcaligata* Smith & Rea; *A. luteovirens* (A. & S. ex Fr.) Gillet (*Armillaria straminea* (Krombholz) Kummer); *A. fusca* A.H. Smith

### Tribus *Collybieae* Konr. & Maubl.

*Icon. sel. Fung.* 6: 29. 1924-37 (ut Collybiées); Imai, *Journ. Fac. Agr. Hokk. Imp. Univ.* 43: 64. 1938.

*Type genus:* *Collybia* Kummer.

*Characters:* Habit collybioid or pleurotoid, more rarely clitocyboid, omphalioid, or almost mycenoid; stipe often insititious; trama monomitic, but often with sclerotized hyphae; hyphae nearly always inamyloid; spores inamyloid, with homogenous wall; gelatinized layers often present in the trama; hymenophoral trama regular to subirregular, never bilateral (excepting the primordia); pigments very variable, sometimes greening with KOH; hymenophore lamellate, but often forked or anastomosing or intervenose, even favoloid, or absent; epicutis neither hymeniform nor with acanthophysoid elements, without pseudoamyloid hairs, but often with a Rameales-structure or an asterostromelloid structure; basidiolles fusoid or not; clamp connections present or absent; if metuloids are present, and the habit is pleurotoid or omphalioid, the hymenophore is alveolar-favoloid; gloeocystidia and latex absent; mycenoid forms lack a basal mycelium and/or clamp connections; omphalioid forms lack a basal mycelium or have a Rameales structure on pileus and/or stipe; setiform cystidia and dermatocystidia are present only in collybioid carpophores; clitocyboid carpophores have no basal mycelium and/or Rameales structure; pleurotoid (but not cyphelloid) forms have clamp connections. Consistency, at least the stipe, somewhat tough, even revivescent, or cartilaginous and hollow in the stipe. On wood, living plants, or vegetable débris, also on moss and lichen thalli, roots etc., saprophytic or parasitic, lichenized (in one species which is pleurotoid and pigmentless), not ectotropically mycorrhizal, but sometimes endotropically mycorrhizal.

The Collybieae contain all genera which, according to the definition of the Tricholomataceae, Resupinateae, Pseudohiatuleae, Panellaeae and Myceneae cannot enter any of these tribus, and are intermediate between the Tricholomataceae on one

hand and the Resupinateae and Marasmieae on the other. For centrally stipitate lamellate forms without pigment, but with basal mycelium, *Hemimycena* should be compared; for those with setiform, dark, shining, insititious, central stipe, *Marasmius* should be compared (see chapter on delimitation under those genera).

#### KEY TO THE GENERA

- A. Cyphelloid genera [hymenophore reduced, not developed in most mature carpophores of a population; habit cyphelloid (cup-shaped), or otideoid (ear-shaped), or spatuloid, more rarely centrally stipitate or with a pseudostipe]. In view of the sometimes somewhat ambiguous affinities of the reduced series, the cyphelloid genera are keyed out in a special key, p. 392).
- A. Agaricoid genera: Hymenophore always well developed, lamellate, or favoloid-alveolar, rarely venose or meruliod.
- B. Carpophores pleurotoid, pigmented, pigment turns partly or entirely green in alkali; carpophores often reviving; stipe lateral or none. *55. Anthracophyllum*, p. 312
  - B. Carpophores not pleurotoid or pigments not turning green in alkali, or stipe merely eccentric.
    - C. Carpophores pleurotoid and trama gelatinized; epicutis an asterostromeloid layer or a Rameales structure; hymenophore consisting of favoloid alveolar angular pores or of radial lamellae which are strongly anastomosing. *60. Campanella*, p. 330
    - C. Carpophores either not pleurotoid or not having an alveolar-favoloid hymenophore; trama gelatinized or not; epicutis a Rameales-structure or a cutis (or dense) or somewhat trichodermial; hymenophore always lamellate, and lamellae intervenose or not.
    - D. Habit clitocyboid or omphaloid, with distinctly decurrent lamellae. Mostly tropical species without gelatinized zones in the trama.
      - E. Pileus with an epicutis which is not a trichodermium of filamentous, entire or distantly branching hyphae, but either a cutis or a poorly (intermittent) trichodermium, the hyphae often irregularly diverticulate (often forming a Rameales-structure); if epicutis trichodermal - lamellae white, gray or cream (not concolorous with pileus); base of stipe insititious, subinsititious or with a (mostly white, silky to fibrillose) basal tomentum; stipe attenuated or equal at the base, more rarely bulbous; a lilac pigment which disappears on drying, *not* present, often no pigment at all. *57. Neoclitocybe*, p. 318
      - E. Pileus with a pigmented trichodermial epicutis which has no Rameales-structure; base of stipe generally with an insititious, socle-base or with basal mycelium; a lilac pigment often present which disappears on drying; carpophores always pigmented. *52. Trogia*, p. 307    - D. Habit collybioid (almost mycenoid) or pleurotoid, i.e. lamellae not deeply decurrent if stipe central. Gelatinous zones sometimes present.
      - F. Habit collybioid (almost mycenoid at times), not pleurotoid.
        - G. Basal mycelium strongly developed, strigose, fibrillose or woolly, white or pigmented. *56. Collybia*, p. 313
        - G. Basal mycelium none or poorly developed and white (subinsititious, rarely thinly silky-tomentose and appressed to the substratum).
          - H. Gelatinized hyphae form definite zones or a definite zone in the trama of the pileus which is therefore duplex, or else the cuticular layer is broadly gelatinized; there is no Rameales-structure in the epicutis, carpophores sometimes rising from black rhizomorphs. *59. Micromphale*, p. 328
          - H. Gelatinized hyphae forming a definite zone in the trama of the pileus or in the broad cuticular layer only if the stipe is insititious or subinsititious and there is a Rameales-structure; if the stipe is only subinsititious or not insititious, there are setiform cystidia and/or dermatocystidia which are pigmented or not and always inamyloid, or a distinct Rameales-structure either on the pileus or the stipe or both, but the base of the stipe is not strongly fibrillose as in *Collybia*, and the white basal mycelium radiates in silky fibrils or a byssus-like covering

around the point of insertion of the stipe in or on the substratum.

58. *Marasmiellus*, p. 320

F. Habit pleurotoid.

- I. Stipe usually lateral, rarely merely eccentric, if lateral - its upper surface not differentiated from the surface or the rear portion of the pileus, most frequently with the habit of a *Panellus (mitis)* or a small *Pleurotus* sometimes stipe entirely absent and then pileus attached laterally; epicutis hyphae, covering of the stipe, cheilocystidia and dermatocystidia (if present) not lacerate (divariculate, short-forked, nodulose, coralloid) but only smooth, entire (or with thin filamentous branches) and smooth cells present; basal mycelium well developed; carpophoroids none; lichenization none. Spores often small and short-ellipsoid to globose, but also ellipsoid and up to 10  $\mu\text{m}$  long.  
J. Habit of a small *Crepidotus*, neither toughish nor fleshy, but trama thin, soft; spores mostly subglobose or globose; cheilocystidia filamentous, sometimes broadened near base, not vesiculose or ampullaceous nor absent; epicutis of loosely arranged but not gelatinized filamentous - often very thin and with acute ends - hyphae, sometimes with inconspicuous filamentous dermatocystidia much like the cheilocystidia; pigment none; pileus smooth, not radially fibrillose, but often lobed, up to 10 mm diam. 54. *Cheimonophyllum*, p. 311
- J. Habit of a laterally stipitate or laterally attached *Pleurotus* or of *Panellus mitis* or *Hohenbuehelia petaloides*, drying rather hard; pileus often reaching more than 20 mm in diameter when mature, glabrous or fibrillose, pigmented or not; cheilocystidia not as indicated above; pseudocystidia sometimes present; epicutis a trichodermium or a cutis, not of remarkably thin-filamentous hyphae if repent, hyphal tips not acute; hyphae of the trama often thickish- or thick-walled. Spores ellipsoid to subglobose, often smaller than 5.5  $\mu\text{m}$ , < 8  $\mu\text{m}$ ; pigment present or absent. 53. *Pleurocybella* p. 309
- I. Stipe usually well-formed, eccentric, more rarely lateral or absent, and then carpophores not with the habit of *Panellus mitis*: epicuticular hyphae mostly arranged in a Rameales-structure, more rarely smooth and filamentous and then stipe insititious or subinsititious and/or either the cheilocystidia or the hyphae of the covering layer of the stipe, at least in part, lacerate (with prongs, frequent forks, ramose-nodulose, diverticulate etc.); basal mycelium none (stipe insititious), more rarely reduced to a few (often unilaterally radiant) cottony-silky, white, appressed fibrils, rarely basal mycelium more strongly developed (and then Rameales-structure well developed either on pileus or on stipe or on the edge of the lamellae); carpophoroids often present; lichenization in one species. Spores rarely under 5, often over 10  $\mu\text{m}$  long.  
K. No Rameales-structure anywhere on the carpophore; pigments present but never incrusting; epicutis trichodermial; pileus deeply divided on a common stipe, or stipe forked, rarely simple, lateral or eccentric; lamellae very narrow, often forked, deeply decurrent; spores 2.5-7  $\mu\text{m}$  long, ellipsoid (see "E" above, *Troglia*).  
K. Not combining the characters enumerated above.
  - L. Lamellae variously attached or concurrent but not decurrent. (See "H" above)
  - L. Lamellae strictly decurrent (see "E" above - *Neoclitocybe*).

## 52. TROGIA Fr.

*Genera Hymenom.* p. 10. 1836.

Type species: *Cantharellus aplorutis* Mont. (= *Trogia montagnei* Fr.).

Characters: Habit clitocyboid to almost omphaloid, rarely pleurotoid (but stipitate), distinctly reviving after having been dried out in situ when remoistened;

pigment always present, sometimes a lilac pigment which disappears on drying, present, then replaced by a brownish-tan or brownish ochraceous pigment which shows in the epicutis-layer, the latter at first trichodermial (but hyphae later often depressed and repent), consisting of at first ascendant, interwoven elements over a subhyaline hypodermium; lamellae almost venose to moderately narrow, arcuate, deeply decurrent, often forked; spore print white; spores small, ellipsoid, smooth, hyaline, inamyloid, acyanophilic; edge of the lamellae homomorphous; cystidia none; basidia normal, basidioles varying from fusoid to cylindric, often remaining sterile (very inconspicuous cystidioles); hymenophoral trama regular to subirregular; subhymenium subcellular; hyphal walls firm to slightly thickened (to 0.8 µm), some hyphae long and voluminous, others filamentous and not inflated, all with clamp connections, inamyloid, not gelatinized. Stipe rather tough to almost leathery, at first solid, either subinsititious or rising from a (frequently tomentose, socle-like) base or pedestal, central, more rarely eccentric to lateral, never with white or black rhizomorphs, but sometimes surrounded by an appressed cotton-like byssus of white mycelium. On wood or woody trash in the subtropical and tropical forest.

*Development of the carpophores:* Gymnocarpous according to Corner and Pegler.

*Area:* Tropics and subtropical zones.

*Limits:* The genus has characteristic features which make it easy to recognize it. Those not familiar with tropical agarics may place it in *Clitocybe* or *Gerronema* from which it differs in its tougher, reviving trama, the trichodermial epicutis, and the characteristic pigmentation. The more interwoven hyphae of the hymenophoral trama and the often forked, narrow lamellae are likewise indicative. *Neoclitocybe* differs by the characters indicated in the key.

Corner's emendation (1966) of this genus is not acceptable to agaricologists. Even the typical species (to which we limit the genus) are not "cantharelloid" in their affinities. The remaining species which Corner transfers to or describes in *Troglia* represent an assemblage of species belonging in *Hemimycena*, *Mycena*, *Gerronema*, *Hydropus*, *Hymenogloea* and probably still other genera which have nothing but the demonstrated or supposed "sarcodimitic" structure in common. This latter is of wide occurrence in the Tricholomataceae. With Corner's definition of *Troglia*, the descriptive data on the species should have filled several times the volume of his treatment of the "cantharelloid fungi" as a whole.

But even the typical *Troglia*s seem to make difficulties in Corner's scheme (1981) where *T. cantharelloides* (Mont.) Pat. is again taken out of *Troglia*, apparently because of the presence of dimitic structure with skeletals in the stipe, a feature Corner did not detect in other *Troglia*s in 1966 because the type specimen was according to him in poor condition or was not seen by him. His remarks "I... find that [P. cantharelloides] is a *Panus*, or, perhaps a *Pleurotus*", are not very enlightening. The species had been fully described by me in *Lloydia* 9: 121. 1946, but dimitic stipe trama was not described. Corner's discovery of dimitic structures in the stipe of *T. cantharelloides* brings up the questions as to how *Troglia* differs from *Pleurotus* and *Panus* and whether *Troglia* should be transferred to the Polyporaceae.

*Troglia* differs from *Pleurotus* in colors and habit, size and shape of the spores. In the white-spored Pleurote the trama is soon di- or amphimitic in pileus and hymenophoral trama, and the few species which have spores as small as *T. cantharelloides* have narrower spores and/or metuloid cystidia. No known *Pleurotus*, by any stretch of the imagination, can be considered related to the Troglas. These differ from *Panus* in hyphal structure of pileus and hymenophoral trama, more consistently thick-walled hyphae in the latter, and can be compared only with sect. *Fulvi* which has hairy or velutinous pileus and stipe, consistently narrower, more elongated spores ( $Q = 2$  or  $> 2$ ), and a little developed subhymenial layer; it usually arises from a pseudosclerotium. All species of *Lentinus* have regular hymenophoral trama, but not one of its species is comparable or close to *Troglia*.

As *Pleurotus* has some distant affinity with *Clitocybe*, *Troglia* may indeed be considered to have some distant affinity with *Panus*. The presence of a violet or amethyst colored pigment disappearing on drying may indeed be identical in some Troglas and some *Pani*. But as *Clitocybe* has much closer affinities with other genera of the same tribus and subtribus of the Tricholomataceae, so, *Troglia* has undoubtedly close affinities with other genera of its tribus, *Collybieae*. The violet pigment found in some fresh specimens of *Troglia* is also present in other genera of Collybieae and, indeed of other Tricholomataceae. The distant affinities between some Polyporaceae and some Tricholomataceae are precisely the reason why both families are here kept in a single suborder and order, in contrast to other classifications referring the Polyporaceae to the Aphylophorales or Polyporales, leaving *Troglia* and the rest of the Collybieae in the Tricholomataceae.

*State of knowledge:* Three species are now known to belong in *Troglia*.

*Practical importance:* Unknown.

## SPECIES

*T. cantharelloides* (Mont.) Pat. (*Panus*, Mont.; *Marasmius purpurascens* Berk. & Curt.; *Hygrophoropsis*, Dennis; *Lentinus scyphoides* Pat.; *L. subscyphoides* Murr.; *Clitocybe sublilacina* Rick); *T. buccinalis* (Mont.) Pat. (*Cantharellus*, Mont.); *T. montagnei* Fr. (*Cantharellus aplorutis* Mont.) unless too close to the preceding species.

## 53. PLEUROCYBELLAA Sing.

*Mycologia* 39: 31. 1947.

*Type species:* *P. porrigens* (Pers. ex. Fr. Sing.)\*

*Characters:* Habit of the carpophores pleurotoid, with a strictly lateral, often scarcely differentiated stipe (which is a protracted inner end of the pileus), rarely with an at first eccentric then lateral or sublateral solid stipe; pileus dry, glabrous, or

\**P. porrigens* is not the type species of the genus *Phylloporus* Karst. (see under *Resupinatus*, p. 339).

finely fibrillose, sometimes concentrically and/or radially grooved, often without any pigment, but also distinctly pigmented, often reaching a diameter of more than 20 mm.; cheilocystidia mostly present, pleurocystidia none, rarely in form of pseudocystidioid bodies which stain strongly in cotton blue; lacerate cheilocystidia, and or true Rameales-structure absent; hyphal system monomitic, with often slightly and irregularly thickened (to 1.8  $\mu\text{m}$ ) or uniformly firm walls, with clamp connections, without gelatinized layers in the trama, inamyloid; hymenophoral trama regular to almost irregular, not metachromatic in cresyl blue and toluidin-blue mount, interwoven, more rarely subparallel, sometimes intermixed with oleiferous hyphae; subhymenium subcellular or appearing so because of the minute, multiseptate elements; epicutis of the pileus - a non-gelatinized cutis with occasional short hyphous excrescences which may be forked or crooked, or with occasional bulges, often the excrescences forming peg-like bodies but not diverticulate or coralloid the cutis often poorly developed and epicutis merely dense and then often a thin trichodermium of filamentous hyphae superimposed. Spore print pure white but sometimes becoming cream on dehydration; spores oblong to short ellipsoid, more rarely subglobose, often very small ( $< 5 \mu\text{m}$ ) but not reaching more than 8  $\mu\text{m}$  in length, smooth, inamyloid, acyanophilic, basidioles filamentous-cylindric to subfusoid; basidia normal in all regards. Veil none. Basal mycelium present. Taste often farinaceous or bitter or acerb. Lignicolous, both on dead and on living wood (Mono- and Dicotyledones, Coniferae).

*Development of the carpophores:* Unknown.

*Area:* Only one species restricted to the temperate regions of the Northern Hemisphere, the others tropical and subtropical.

*Limits:* The genus was originally limited to *P. porrigens*. However, as more species became known, the limits between the genera *Nothopanus* and *Pleurocybella* became difficult to trace and the hiatus too small to separate these genera. On the other hand, the type species of *Nothopanus* turned out to be a *Pleurotus* (see Singer & Kuthan, *Ceská Mykologie* 34: 71. 1980). *Cheimonophyllum* and *Marasmiellus* are easily distinguishable if the key characters are considered carefully. The pleurotoid forms of *Clitocybe* have a well developed stipe with decurrent lamellae. If the lamellae are not strictly decurrent, the species belongs nevertheless to *Clitocybe*, if the stipe is merely eccentric and large ( $24-35 \times \pm 6-8 \text{ mm}$ ), and the taste mild.

While it is easy to distinguish *Pleurocybella* from all genera of the Tricholomataceae, it must be understood that it is somewhat ambiguous between *Clitocybinae* and *Collybieae*. With the stipe reduced or lateral as in *Pleurocybella*, we cannot find any similarity between *Clitocybinae* and *Pleurocybella* as far as habit is concerned. On the other hand, in the *Collybieae* strongly pleurotoid species, even completely stipeless species are known, and Kühner, in his tribus *Nothopaneae*, genus *Nothopanus*, considers *P. porrigens* and *Cheimonophyllum candidissimum* congeneric, placing them in two subgenera of the same genus. For these reasons we maintain *Pleurocybella* in the same position as *Nothopanus* was formerly placed rather than to return it to the neighborhood of *Clitocybe* where it was originally placed.

Kühner (1980) inserts, aside from *Pleurotus*, *Lentinus*, and *Panus*, also *Schizophyllum*, *Resupinatus*, *Nothopanus*, *Cheimonophyllum*, and *Pleurocybella* in his family

Pleurotaceae - an assembly of unrelated genera, including also *Geopetalum*, *Tectella* and *Panellus*.

**State of knowledge:** The type species is well known. Five additional species are best classified with it.

**Practical importance:** Unknown.

## SPECIES

*P. porrigens* (Pers. ex Fr.) Sing.; also *P. vinosofusca* (Bres.) Sing. (*Xerotus*, Bres., *Hedwigia* 56: 290. 1915) and other species formerly (Singer 1975) indicated under *Nothopanus*: *N. panelloides* (Dennis) Sing.; *N. amarescens* Sing.; *N. tropicalis* Sing. and *N. noctilucens* (Lév.) Sing.

### 54. CHEIMONOPHYLLUM Sing.

*Sydowia* 9: 417. 1955.

**Type species:** *Agaricus candidissimus* Berk. & Curt.

**Characters:** Habit pleurotoid (of a small *Crepidotus* or *Panellus mitis*), without a stipe or with a strictly lateral one (not differentiated from the pileus when seen from above), pileus not over 20 mm broad, entirely without pigment, smooth, soft; lamellae neither excessively crowded and narrow nor deeply decurrent or much forked; epicuticular hyphae narrowly filamentous; cheilocystidia and occasional dermatocystidia filamentous, often once branched into thin-filamentous branches, loosely arranged, the hyphal ends often acute; hymenophoral trama regular, not gelatinized; subhymenium denser than the trama, rameous; hyphae strictly monomitically arranged, inamyloid, with clamp connections. No Rameales-structure anywhere, but surfaces occasionally with narrow hyphous or small subisodimetical or knotty outgrowths in some specimens. Spore print (fresh) pure white. Spores small to medium, globose or subglobose, with thin to somewhat thickened, homogenous, smooth wall which is inamyloid and acyanophilic, sometimes vaguely rounded-angular. Basidia normal, but occasionally some sclerobasidia differentiated; basidioles not fusiform. Pleurocystidia none. Odor none. On wood and other vegetable matter (débris), attached with white basal mycelium.

**Development of the carpophores:** Unknown.

**Area:** Probably almost cosmopolitan, certainly in Europe, North America, neotropics, and south to the Southern temperate zone.

**Limits:** The genus can be distinguished from others by the key characters. The soft structure suggested to me relationship with the Paxillaceae, but the acyanophilic spores were already indicated by Kotlaba & Pouzar (1964) as showing that this genus is not paxillaceous. It is obviously closely related to *Pleurocybella* and *Marasmiellus*.

*State of knowledge:* Only two species are known, a third one is doubtful.

*Practical importance:* Unknown.

## SPECIES

*C. candidissimum* (Berk. & Curt.) Sing.; *C. stypticoides* (Speg.) Sing.; perhaps also *Pleurotus dictyorhizus* (D.C. ex Fr.) Gillet (sensu Josserand).

### 55. ANTHRACOPHYLLUM Ces.

*Myc. Borneo*, p. 3. 1879.

*Type species:* *A. beccarianum* Ces.

*Characters:* Pileus laterally attached, rarely with a stipe which, however is not visible from above in most species when they have reached maturity; cuticle of the pileus little or not differentiated, dry, rough under the microscope (Rameales structure), old specimens usually more or less grooved on the surface of the pileus, at least its margin along the interlamellar spaces; lamellae distant, intermixed with lamellulae, with entire edge, deep colored even in fresh specimens, more so in dried material, wedge-shaped with acute edge; hymenophoral trama subregular-subirregular, with a distinct axillar trend, but the hyphae either individually or in strands strongly interwoven in all directions, narrower than in the trama of the pileus; spores hyaline, but often colored (the cell sap) from the dissolved pigments in KOH (greenish or cinnamon); mostly broadly cylindric but also ellipsoid or oblong to fusoid, smooth, acyanophilic, inamyloid, thin-walled; cystidia none of any kind except for pseudoparaphyses which are scattered on the edge and the sides of the lamellae and often slightly thick-walled; basidia normal in all regards, but the sterigmata (usually 4) sometimes deformed and saccate (inability to discharge the spores?); subhymenium present, dense and rameose; pigments very characteristic in the hymenophore, one, bronwih cinnamon to deep mahogany red is extracted by alcohol, and also escapes in preparations with KOH (medium becomes cinnamon or mahogany for a short while after the fragment is immersed); there are also carbonaceous particles, most of them clinging to the walls of the basidia and hyphae, sometimes even the spores; they become blue-green in KOH and the greenish solution resulting from it dyes the whole tissue, especially the subhymenium and the basidia, green; context with fewer carbonaceous pigment bodies, thin, consisting of thick-walled, interwoven, inamyloid hyphae with numerous clamp connections. Veil none. Mostly on wood.

*Development of the carpophores:* Unknown.

*Area:* Tropics; in some regions penetrating into the warmer belt of the temperate zones.

*Limits:* This genus has been confused with *Xerotinus* which is closely related to *Gloeophyllum* and belongs to the Aphylophorales (Pl. 42).

*State of knowledge:* A rather large number of species has been described, all of them very much alike in dried condition. Lloyd who has studied most of the types, arrived at the other extreme, thinking that they were all one species. The truth is according to the experience of the author who has studied the types of *Xerotinus nigrita*, *X. lateritius*, *X. viticola*, *X. discolor*, *X. berterii*, *X. fuliginosus*, most probably somewhere in the middle. A complete monograph of the species should include more dependable data from the fresh specimens, and the development of the carpophores of at least one species. At present, the author recognizes 5 species.

*Practical importance:* The species of this genus must be considered as wood destroyers. The damage they inflict is probably of little economic consequence.

## SPECIES

*A. nigrita* (Lév.) Kalchbr. (*Xerotinus*, Lév.; *A. beccarianum* Ces.; ?*Panus melanophyllum* Fr.); *A. lateritium* (Berk. & Curt.) Sing. (*Xerotinus*, B. & C.; *Plicatura*, Murr.; *Xerotinus fuliginosus* Berk. & Curt.; *Xerotinus viticola* Berk. & Curt.); *A. discolor* (Mont.) Sing. (*Xerotinus*, Mont.; *Crepidotus xerotoides* Speg.); *A. berterii* (Mont.) Sing. (*Xerotinus*, Mont.); *A. paxilloides* Sing.; apparently also *A. proximum* (Bk. & Br.) Reid and *A. archeri* (Berk.) Pegler.

## 56. COLLYBIA Kummer

*Führ. Pilzk.*, p. 26. 1871, n. cons. ut *Collybia* "(E.M. Fries) Staude".

*Type species:* *Collybia tuberosa* (Bull. ex Fr.) Kummer (see *Schweiz. Zeitschr. f. Pilzk.* 29: 208. 1951).

*Syn.:* *Agaricus*, tribus *Collybia* Fr., *Syst. Mycol.* 1: 129. 1821.

*Collybia* (Fr.) Quél., *Champ. Jura Vosges*, p. 92. 1872.

*Sclerostilbum* Povah, *Mycologia* 24: 242. 1932 (imperfect form of *Collybia* cf. Lütjeharms, in *Flora Batava* 1936).

*Dictyoploca* (Mont. ut tribus, nom. subnud.) Heim, *Rev. Myc.* 10: 23. 1945, nom. subnud.

*Rhodocollybia* Sing., *Schweiz. Zeitschr. Pilzk.* 17: 1. 1939.

*Microcollybia* Métrod *Rev. Mycol.* 17: 75. 1952, nom. subnud. ex Lemox, *Mycotaxon* 9: 187. 1979.

*Characters:* Carpophores strictly collybioid to marasmoid in habit, i.e. lamellae not distinctly decurrent but adnexed to subfree, or sinuate to emarginate, or planely adnate; margin initially usually incurved; pileus often hygrophanous, never viscid, not conico-campanulate but convex to flat, sometimes somewhat depressed but not strongly umbilicate in most species; stipe thin and rather tough to very tough, not string-like, more rarely somewhat thicker but then distinctly fibrous-toughish and soon becoming hollow; pileus without strongly differentiated epicutis, i.e. no sphaerocysts (epithelium), erect elements in palisade (trichodermial palisade,

hymeniform layer' but often with some kind of modified hyphae (nodulose-ramose to diverticulate - *Rameales*-structure), the cuticle usually consisting of a denser layer of intricately interwoven, or repent, subparallel to parallel hyphae which are then radially arranged; hymenophore lamellate, often developing cyanic acid; hymenophoral trama regular or subregular (i.e. hyphae often very strongly interwoven), consisting of rather thin-filamentous hyphae; basidia generally normal in all respects, rather small; basidioles often fusoid; cheilocystidia absent, or present, and then often inconspicuous and appearing on mature specimens, directly from the hyphae of the trama; other cystidia none; spores from globose to ellipsoid to ovoid to fusoid to cylindric to claviform-oblong, with thin, under the light microscope smooth (Pl. 48, 3-5) acyanophilic inamyloid walls, only in sect. I in some specimens walls of many spores cyanophilic and pseudoamyloid, with or without suprahilar depression; spore print pure white, pale cream color, or often cream-pink (Séguy 200, Crawshay, shay D, Ridgway's "seashell pink") sometimes cream-white but becoming pinkish cream in the herbarium "oyster white" M. & P. e.gr. in sect. 3) stipe sometimes developing from sclerotia, sometimes forming conidia on the covering layer, never insititious, smooth or longitudinally striate to sulcate, glabrous, pruinata, or velvety; pseudorhiza often present; context fleshy-tough or fleshy-fibrous, or sometimes plainly tough and reviving after the carpophores have dried out in situ, consisting of thin or thick walled hyphae, often both thin and thick-walled hyphae in one carpophore, the hyphae pigmented in many forms, the pigment either intercellular or membranal or intracellular, the hyphal walls never amyloid, all hyphae with clamp connections; gloeo-vessels none but a few oleiferous hyphae occasionally present; latex none; taste mild or peppery; odor none, or characteristically of sauerkraut, of HCN (*Collybia dryophila*), or of dried celeriac, or garlic. On the soil, on needles or foliage or fungi decaying on the ground, or among deep moss, on decaying or rather fresh wood, often on humus in ruderate places, on lawns, in gardens, etc.

*Development of the carpophores:* Gymnocarpous (*C. dryophila*, *confluens*, *tuberosa*); stipitocarpous.

*Area:* Cosmopolitan, excepting Antarctica.

*Limits:* Species with distinctly decurrent lamellae do not belong to *Collybia*, even though the characters of the stipe may fit in the diagnosis of *Collybia*. Species with rough spores do not belong in this genus but, if the spore print is pink, rather in *Lepista*, or *Rhodocybe*. However, there is no doubt that the species with pinkish spore print in *Collybia* may be rather similar to these genera; they can be distinguished by their more collybioid habit, the tougher stipe, the smooth, acyanophilic spores, and the odor. Species seemingly belonging in *Collybia* with pseudoamyloid spores should not be confused with *Hebelomina*.

The genus *Collybia* was formerly a completely artificial group, poorly delimited from *Marasmius*, *Marasmiellus*, not well distinguished from *Oudemansiella*, *Xerula*, *Flammulina*, *Tricholomopsis*, *Micromphale*, and *Pseudobaeospora*; and often confused with the group of genera that was then incorporated in *Mycena* and *Omphalia*. The characters of the epicutis clearly separate *Collybia* from nearly all

species of the *Marasmieae*; this made it possible to revise the limits of *Collybia* against *Marasmius* and allied genera. One species of *Collybia* was then transferred to *Tricholomopsis* because of the more conspicuous cheilocystidia, more tricholomatoid habit, and the absence of affinities in *Collybia*.

As for the delimitation of *Collybia* against *Clitocybe*, see there. We do not admit in *Collybia* any species with rancid mealy odor and glaucous FeSO<sub>4</sub>-reaction. This means that the *Farinolentes* formerly included in *Collybia* by this writer had to be transferred to *Clitocybe*. The generic separation of sect. 1 (as *Rhodocollybia*) and 9 (as *Microcollybia*) is not justified inasmuch as the main differentiating characters are inconstant; besides "*Microcollybia*" in case of acceptance would become *Collybia* (proper) for nomenclatorial reasons.

*State of knowledge:* *Collybia* is a comparatively well-known genus in Europe and Eastern North America\* yet a world monograph would probably bring out a clearer picture of the various species belonging here. Certain groups, especially the tropical and generally non-European species are in need of revision. The exact color of the spore print, the exact arrangement of the cuticular hyphae and the microscopical characters such as spore size and shape, localization of the pigments, and finally chemical characters will be helpful. The odors are rather characteristic in this genus, and so is the taste of the context in at least two species. The author admits only 74 species but more will eventually remain in or be transferred to *Collybia*, and some more, mainly tropical species are still undescribed, or in need of additional observations.

*Practical importance:* Negligible according to the available data for most species but some *Subfumosae* may be parasitic on cultivated plants and *C. confluens* contains an alkaloid (Tyler & Stuntz) whose pharmacological importance is unknown. Also *C. peronata* contains muscarine and epimuscerine (*Helv. Chim. Acta* 59: 2434. 1976).

## SPECIES

Sect. 1. *STRIIPEDES* (Fr. ut sect. tribus *Collybiae*) Quél. (1872-3 = subgen. *Rhodocollybia* (Sing.) Halling 1983). Stipe often rather thick, more or less longitudinally striate or sulcate; spore print usually more or less cream pink, said to be white in *C. prolixa*; spores often pseudoamyloid and cyanophilic.

*Type species:* *C. fusipes* (Bull. ex Fr.) Quél.

Stirps *Maculata* (pseudorrhiza present or absent; context of the pileus rather thick; cuticle dry; odor of celeriac, or none).

*C. maculata* (A. & S. ex Fr.) Kummer; *C. pinicola* (Murr.) Sing. (Melanoleuca, Murr.); *C. collybiiformis* (Murr.) Sing. (Melanoleuca, Murr.); *C. distorta* (Fr.)

\*This is thanks to the modern treatment of the Collybias in Kühner & Romagnesi (1953, under *Collybia*, sect. A, C and *Marasmius*, sect. H p.p., I) and the excellent recent monograph by Halling (The genus *Collybia*..., *Mycologia, Memoirs* no 8, 1983).

Quél.; *C. margarita* (Murr.) Sing. (*Melanoleuca*, Murr.); *C. murrilliana* Sing. [*Melanoleuca maculata* Murr.;? *C. maculata* var. *immaculata* (Cooke) Sacc.]; *C. westii* (Murr.) Sing. (*Melanoleuca*, Murr.); also the following fungi which are closely related and perhaps not all specifically different: *C. maculata* var. *immutabilis* A.H. Smith, *C. leucocephalooides* (Peck) Sing., *Tricholoma* (Peck) and *Melanoleuca* (non *Collybia*) *unakensis* Murr.; probably also in this stirps: *C. bakerensis* A.H. Smith; *C. prolixa* (Hornemann ex Fr.) Gill. may belong here (but spore print white).

Stirps *Butyracea* (pseudorrhiza none or little developed; pileus rather thin; cuticle somewhat opimous; odor of cyanic acid or none).

*C. butyracea* (Bull. ex Fr.) Quél. [including *f. asema* (Fr.) Sing.]; also *C. albistricta* (Murr.) Murr. (*Gymnopus mammillatus* Murr.); *C. tucumanensis* Sing. (if spore print pink).

Stirps *Fusipes* (perennial pseudorrhiza present; growing on the base of trees).

*C. fusipes* (Bull. ex Fr.) Quél. [*C. lancipes* (Fr.) Gillet]; here probably also *C. subsulcatus* A.H. Smith.

*Note:* Stirps *Fusipes* with *Dryophila*-type of epicutis and inamyloid spore wall has been separated from the rest of sect. 1 by Cléménçon (1981) and Halling (1983). In this case it must be understood that *C. fusipes* (stirps *Fusipes*), as type species of the section, must remain in sect. *Striipedes* and the other species must be transferred to section *Maculatae* Lennox ex Halling, 1983. Since *C. butyracea* is frequently found to have only a minority of weakly pseudoamyloid and a majority of inamyloid spores, this situation shows the difficulty of defining the sections of *Collybia*, and, as Halling correctly states, the continuity of the section *Striipedes* (as here accepted) and sect. *Collybia*, in other words the generic integrity of *Collybia* becomes evident.

Sect. 2. *CYSTIDIATAE* Sing. (1961). Differing from section 1 and 5 in whitish spore print and broad (>7 µm), characteristically clavate to clavate-vesiculose cheilocystidia present from the beginning, some occasionally also somewhat away from the lamella edge proper. The spore print becomes cream by dehydration.

*Type species:* *C. sleumeri* Sing.

*C. sleumeri* Sing.; also *C. sacchari* (Sing. in Sing. & Digilio) Sing.; apparently *C. crassipes* (Schaeff. ex Fr.) Moser sensu Moser, Cléménçon, non Schaeffer (which is obviously *Tricholomopsis platyphylla*).

Sect. 3. *DICTYOPLOCAE* (Mont. ut tribu, *nom. subnud.*) Sing. Stipe very slightly sulcate-striatulate, almost smooth, glabrous; spore print creamy white when fresh but becoming pinkish cream in the herbarium; pileus white or fuscidulous to violet; lamellae slightly to often strongly venose-anastomosing.

*Type species:* *C. plectophylla* (Mont.) Sing.

*C. plectophylla* (Mont.) Sing. (*Marasmius*, Mont. cf. *Marasmius argentinensis* Speg.).

Sect. 4. *IOCEPHALAE* Sing. ex Halling (1983). Pigment purplish, typically turning pink with acids, blue or violet with alkalis; lamellae normally not strongly anastomosing.

Type species: *C. iocephala* (Berk. & Curt.) Sing.

*C. iocephala* (Berk. & Curt.) Sing. (Marasmius, B. & C.); also *C. syringaea* Sing. unless to *Pleurocollybia*.

Sect. 5. *LEVIPEDES* (Fr.) Quél. (1872-3). Pileus not colored as in sect. 3; stipe smooth and glabrous to white pruinose or white pubescent or with ochraceous to fulvous brown or deep brown strigosity in lower portion of stipe except for the basal tomentum; spore print white, rarely palest cream white, especially after desiccation, not cream pink when fresh; lamellae normally not strongly anastomosing; epicutis strongly reduced, therefore uppermost layer of pileus cuticle as seen in scalp preparation of partly broad, frequently branching, but not diverticulate hyphae, not radially arranged ("Dryophila-structure").

Type species: *C. dryophila* (Bull. ex Fr.) Kummer.

*C. dryophila* (Bull. ex Fr.) Kummer, with several varieties; *C. marasmoides* (Britz.) Bresinsky & Stangl (Marasmius bresadolae Kühn. & Romagnesi; *C. kuehneri* Sing. *Collybia*, Sing.); *C. peladae* Sing.; *C. phylladophila* Sing.; *C. konradiana* Sing.; *C. fuscopurpurea* (Pers. ex Fr.) Kummer (Marasmius, Fr.); *C. alkalivirens* Sing. (C. *obscura* Favre); *C. spongiosa* (Berk. & Curt.) Sing.; *C. semihirtipes* (Peck) Halling (if not too close to the preceding species); obviously also *Collybia hybrida* (Kühn. & Romagnesi) Svrcek & Kubicka (Marasmius, K. & R.) and *C. hepatica* (Berk.) Pegler.

Sect. 6. *VESTIPEDES* (Fr.) Quél. (1872-3) (Marasmius, sect. Peronati, Kühner 1934). Stipe neither fully glabrous nor distinctly longitudinally sulcate but almost entirely or entirely pruinose, villous, tomentose or stigose; spore print pure white to pale flesh color (unknown in many species); epicuticular hyphae well developed and usually narrow, filamentous, generally distinctly radially arranged, not diverticulate or cauliflower-like (no *Rameales*-structure and no *Dryophila*-structure).

Type species: *C. confluens* (Pers. ex Fr.) Kummer.

*C. peronata* (Bolt. ex Fr.) Kummer; *C. cylindrospora* Kauffm.; *C. confluens* (Pers. ex Fr.) Kummer (*C. hariolorum* (D.C. ex Fr.) Quél. sensu Fr. non Kühner & Romagn. as Marasmius; *A. archyropus* Pers.; *A. sagarum* Pers.); *C. ingrata* (Schum. ex Fr.) Quél. (unless too close to the preceding species); *C. lindquistii* Sing.; *C. porrea* (Pers. ex Fr.) Kummer; *C. impudica* (Fr.) Sing.; *C. putila* (Fr.) Sing.; *C. collybioides* (Speg.) Sing.; *C. platensis* (Speg.) Sing.; *C. subhybrida* Sing. in Sing. & Moser; *C. piperata* (Beeli) Sing.; *C. phoebophila* Sing.; *C. fuegiana* Sing.; *C. ushuvayensis* (Speg.) Sacc.; *C. alboavellanea* Sing.; *C. pulchella* (Berk.) Sing.; *C. neotropica* Sing.; *C. paranaguae* Sing.; *C. njalaensis* (Beeli) Pegler (*C. brunneosetosa* Dennis); *C. benoistii* Boudier; *C. luxurians* Peck; *C. praealpina* Sing. (nom. nov. = *C. hariolorum* "D.C." Bres., Icon. Myc. 5: 202. 1928 vix al.); *C. griseolobrunnea* (Sing. in Sing. & Dig.) Sing.; *C. mucubajiensis* Denn. (*C. urubambae* Sing.).

**Note:** Either to this or the following section: *Marasmius dulcis* Beeli. - Either to this or the preceding section: *C. acicola* Sing.; *C. apiahyina* Speg.; *C. polygramma* (Mont.) Sing.; *C. hemileuca* (Berk. & Curt.) Sacc.

Sect. 7. *SUBFUMOSAE* Sing. Characters as in the preceding section but hyphae of the strongly developed epicutis showing a more or less distinctly developed "Rameales-structure", i.e. hyphae nodulose-coralloid to diverticulate or repeatedly forked with thin side-branchlets, hyphae generally irregularly recurved or intricately interlaced, especially so in age, young often with a still poorly developed Rameales-structure (i.e. with few branchings and projections); hymenial cystidia sometimes present, in other species absent; stipe generally as in the preceding section but at times subglabrous.

*Type species: Collybia subfumosa* Speg.

*C. subfumosa* Speg.; *C. paurospora* (Sing.) Sing. (Marasmiellus, Sing. 1958); *C. castaneidiscus* (Murr.) Murr.; *C. fascicularis* (Rick ex Sing.) Sing. (Marasmiellus, Rick ex Sing.); *C. distortiformis* (Sing.) Sing. (Marasmiellus, Sing.); *C. fibrosipes* (Berk. & Curt.) Dennis (Marasmius, Berk. & Curt.); *C. bifor-  
mis* (Peck) Sing. (Marasmius, Peck); *C. domestica* (Murr.) Sing. (Marasmius, Murr.); *C. flavomycelina* Sing.; *C. batistae* Sing.; *C. contraria* (Peck) Halling (C. umbonatella Sing.); *C. dichroa* (Berk. & Curt.) Gilliam; *C. praeacuta* (Ell.) Gilliam; *C. polyphylla* (Peck) Sing.; *C. vindobonensis* Höhn.

Sect. 8. *IXOTRAMA* Sing. (1972). Differing from the preceding sections in having a strongly gelatinizing infrahypodermial layer, often knotty cheilocystidia and a sparse, weak Rameales-structure in the epicutis; differs from the genus *Micromphale* in the strongly developed basal mycelium.

*Type and only species: C. ixotrama* Sing.

Sect. 9. *COLLYBIA* (*Cirrhatae* Sing. 1943). Stipe not sulcate, finely pruinate pubescent or with conidiophores; pileus white or whitish in moist condition, at least in the broad marginal zone, very thin-fleshy, rather small and membranaceous; stipe racemose and/or rising from a sclerotium, more rarely neither racemose nor rising from a sclerotium; cheilocystidia none, or very inconspicuous. Frequently on decaying Basidiomycetes.

*Type species: C. tuberosa* (Bull. ex Fr.) Kummer.

*C. cirrata* (Pers. ex Pers.) Quél.; *C. cookei* (Bres.) J.D. Arnold; *C. tuberosa* (Bull. ex Fr.) Kummer; *C. racemosa* (Pers. ex Fr.) Quél. (*Sclerostilbum septentrionale* Povah, sclerotial and conidial form).

## 57. *NEOCLITOCYBE* Sing.

*Sydotia* 15: 55. 1961.

Syn.: *Ossicaulis* Redh. & Ginnns, *Trans. Myc. Soc. Japan* 26: 362. 1985.

*Type species: N. byssiseda* (Bres.) Sing.

**Characters:** Habit clitocyboid to omphaloid, rarely somewhat pleurotoid because of eccentric stipe; lamellae distinctly and mostly deeply decurrent; either the pileus

shows a distinct *Rameales*-structure, or the stipe is subinsititious or insititious; spores smooth, of variable shape and size but generally subglobose, ellipsoid, guttiform, or oblong to cylindric and *not* with outgrowths or subangular-stellate, inamyloid, acyanophilic. Basidia bisporous or tetrasporous, and normal, in one species with excessively long cylindric sterigmata, in another excessively long only in certain collections (in others of normal size); basidioles generally fusoid as in *Marasmiellus*; hyphae thin- to thick-walled, inamyloid, with clamp connections, not gelatinized; hyphal system monomitic (mostly of the type described by Corner as sarcodimitic); hymenophoral trama regular, its hyphae subparallel to rather strongly interwoven (almost subirregular). Epicutis with often poorly developed (weak or intermittent) *Rameales*-structure, - a cutis or a trichodermium (and then with intracellular pigment). On earth, but generally in the forest, or on various débris, most frequently lignicolous.

*Development of the carpophores:* Unknown.

*Area:* Almost cosmopolitan, not rare in northern North America but one species in Central Europe, some in Patagonia, and many in the tropics and subtropics. Only in forested areas.

*Limits:* The species of *Neoclitocybe* have in the past often been mistaken for either *Clitocybe* or "Omphalia", or else for *Marasmiellus* or *Trogia*.

Like *Pleurocybella*, *Neoclitocybe* is intermediate between *Clitocybe* and *Marasmiellus*. *Neoclitocybe* differs from *Clitocybe* in the subinsititious to insititious base of the stipe, or, if the stipe has a distinct basal mycelium, in the *Rameales*-structure of the epicutis. Some species with a weak *Rameales*-structure and a byssus-like mycelial covering appressed to the substratum and not extensive, but often accompanied by white rhizomorphs, are difficult to distinguish from *Clitocybe* sect. *Vernae*, but these species have a farinaceous taste and odor, a rather subtropical to tropical area of distribution, and less abundant, white rhizomorphs. *Marasmiellus* differs from *Neoclitocybe* in the habit of the carpophores (collybioid, sometimes almost mycenoid, often pleurotoid versus clitocyboid-omphalioid) and is not likely to be confused with *Neoclitocybe* in the field. *Trogia* can be very similar to *Neoclitocybe*, particularly in the case of species with trichodermial epicutis (like *N. aprilis*), but in this case the colors are quite different (especially the lamellae in youth never white in *Trogia*) and the lamellae are not quite as narrow as in *Trogia*, nor is there ever a socle-like base. The genus *Gerronema* has a better developed basal mycelium than those *Neoclitocybes* which have an indistinct *Rameales*-structure, and the epicutis in all *Gerronemas* is composed of smooth, simple hyphae. Somewhat pleurotoid carpophores are sometimes observed in *Neoclitocybe* but in this case the deeply decurrent lamellae differentiate them from those of *Marasmiellus*. In one species (*N. portentosa*) the pigments turn green in KOH as they do in *Anthracophyllum*, but here the lamellae are "slate" M & P and close, and the pigment turns a beautiful amethyst color in HCl, and the stipe is not lateral but merely varying between central and eccentric.

*State of knowledge:* All species enumerated below have been studied sufficiently to confirm their affinity with the type species and their insertion in *Neoclitocybe* as

defined here. A key to the species then known has been published by Singer & Grinling (1967). We admit now 17 species.

**Practical importance:** At least two species (*N. acromelalga* and *N. alba*) are poisonous, with very characteristic symptoms.

## SPECIES

*N. byssiseda* (Bres.) Sing.; *N. lifotama* Sing. in Sing. & Grinling; *N. alba* (Velen.) Sing. (Omphalia alba Velen, *Nov. Myc. Nov.* p. 41. 1947, *N. alnetorum* (Favre) Sing.); *N. euomphala* (Berk.) Sing.; *N. microspora* Sing.; *N. aberrans* Sing.; *N. substenophylla* (Murr.) Sing.; *N. nivea* (Rick) Sing.; *N. nauseosa* (Rick) Sing.; *N. subnimbata* (Rick) Sing.; *N. latispora* Sing.; *N. viridilutea* (Rick) Sing.; *N. infundibuliformis* (Berk. & Br.) Sing.\* (*Trogia*, B. & Br.; *N. membranacea* Sing. & Grinl.; ?*Trogia violaceogrisea* (Henn.) Pat.); *N. omphalina* (Sing. in Sing. & Digilio) Sing.; *N. myceliosa* Sing.; *N. portentosa* Sing.; *N. acromelalga* (Ichimura) Sing.\*\*; *N. aprilis* (Sing. in Sing. & Digilio) Sing.; apparently also *Marasmius omphaliformis* Kühner and the type of *Clitocybe peralbida* Murr. and that of *C. pulchella* Speg.; according to Reid (1975) also *N. chortophila* (Berk.) Reid.

## 58. MARASMIELLUS Murr.

*North American Flora* 9(4): 243. 1915.

**Type species:** *M. juniperinus* Murr.

Syn.: *Pterospora* Métrod, *Prodr. fl. mycol. Madagascar* 3: 140. 1949 non Nut. 1821 (Pyrolaceae)

**Characters:** Habit marasmoid-collybioid or mycenoid, also frequently pleurotoid, revivescent or putrescent; some species forming carpophoroids and/or protocarpic tubers. Pileus glabrous, subtomentose, tomentose flocculose, not glutinous. Hymenophore lamellate, variously attached to the stipe, often intervenose but not favoloid-anastomosing, mostly intermixed-inserted but lamellulae sometimes very few or none, rarely in some specimens of a population hymenophore strongly reduced. Stipe central, eccentric, lateral or absent, unshining or at the utmost with a dull shine underneath a pruinate, pubescent, flocculose or tomentose covering, but eventually often glabrescent, not black and seta-like, insititious or subinsititious, rarely with a fibrillose-tomentose basal mycelium but then the epicutis with a distinct *Rameales*-structure and/or stipe eccentric to lateral. Context either not at all gelatinized or with gelatinized (i.e. thin-walled hyphae imbedded in a gelatinous mass) zones and/or pockets but then always with non-anastomosing lamellae and fusoid basidioles (in pleurotoid species) and with a distinct *Rameales*-structure (if collybioid). Odor usually not characteristic, rarely strong (of sauerkraut or of

\*c.n. (*Trogia infundibuliformis* Berk. & Br., *J. Linn. Soc., Bot.*, 14: 45. 1875).

\*\*c.n. (*Clitocybe acromelalga* Ichimura, *Bot. Gaz.* 65: 110. 1918.)

garlic). Epicutis typically a *Rameales*-structure, i.e. of lacerate elements with knobs, diverticula and short ramifications, as characteristic of section *Rameales*, but this structure often poor or weak and in a minority of species not any more recognizable as a *Rameales*-structure but replaced by mostly thin, mostly densely interlaced hyphae or a cutis-like structure, not gelatinized even if the underlying trama is gelatinized; hyphae inamyloid, with or more rarely without clamp connections, not forming chains of very voluminous cells. Basidioles most or all fusiform or subfusiform, rarely in otherwise typical forms with a majority of clavate-cylindrical basidioles; cystidia always either like the cheilocystidia or similar, or else pseudoparaphysoid, or absent; cheilocystidia usually numerous, rarely rare or scattered, gloeo-, chryso- and macrocystidia never present; covering of the stipe like that of the pileus or containing dermatocystidia or hairs, often hairs like those of *Crinipellis* (but inamyloid). Spore print pure white to pale cream. Spores small to large, narrow to broad, with thin, inamyloid, homogenous wall, acyanophilous, smooth, sometimes dimorphic, sometimes (sect. *Nigripedes*) tetrahedric or cross-shaped or merely with an eccentric bulge or spur on the outer side (much like in some *Campanellae*). On living and, more often, dead vegetable matter, particularly branches, trunks, logs, roots, culms, leaves or leaf petioles or fruits of Coniferae, Mono- and Dicotyledones, mostly trees and shrubs, but also herbs, rarely on seemingly amorphous humus or sand, on dead mosses or on Pteridophyta. Most species thermophilous, but many occur also in the temperate zones of both hemispheres. At least one species is lichenized.

*Development of the carpophores:* Paravelangiocarpous and pileo-stipitocarpous (*M. albuscorticis* and *M. ramealis*) but some might be mono- or bivelangiocarpous or gymnocarpous.

*Area:* Almost cosmopolitan (absent in Antarctica).

*Limits:* The genus *Marasmiellus* was originally proposed for membranous species with white spores and eccentric stipe, whereas the centrally stipitate species were originally (by Fries 1838) placed in *Marasmius* but later separated (by Singer) from that genus and temporarily combined with *Hemimycena*, later with *Marasmiellus*. There can be no doubt but that there is no sharp line or hiatus between the pleurotoid and the centrally stipitate forms nor is there any correlation of this character with presence or absence of a *Rameales*-structure. It may be stated here that in some species the stipe is central in young, eccentric in old specimens, and the *Rameales*-structure present in old, absent in young specimens, or in certain areas of the pileus. I find therefore no grounds for a recent attempt (Horak, 1968) to separate *Collybiopsis* (with the supposed type species *C. ramealis*) from *Marasmiellus* sensu stricto even if the typification of *Collybiopsis* by Earle (1909) were legitimate which it is not according to Singer (1951) and Donk (1962) who recognized *M. scorodonius* resp. *calopus* as the type.

The generical characteristics of *Campanella* - shape of basidioles, shape of hymenophore - differentiate this genus rather well from *Marasmiellus* although one may point out some species in both genera which seem to show a clear affinity

between them; this holds particularly true if we realize that we have only to compare the species with gelatinized trama in *Marasmiellus*.

The genus *Marasmiellus* differs from *Marasmius* in the structure of the epicutis of the pileus and the inamyloid hyphae (even in the stipe). The genus *Collybia*, one section of which shows the same structure of the epicutis as known in *Marasmiellus* sect. *Rameales*, can be distinguished by the strong development of the basal mycelium in form of an extensive fibrillose or tomentose to strigose myceloid mass, or else the development of pseudorrhizae or sclerotia. That minority of Marasmielli which shows a slight development of the basal mycelium differs strongly from all known *Collybiae*, particularly because this phenomenon is observed mainly in the pleurotoid and pleurocystidiate *Marasmielli* whereas pleurotoid and pleurocystidiate *Collybiae* are exceptional. Likewise, the basal mycelium permits distinguishing *Gerronema* from *Marasmiellus*, but the mostly omphaliod habit of the former would not easily lead to confusion with *Marasmiellus*. Some *Gerronemas* were formerly thought to belong to *Marasmiellus* but this was an error, soon corrected, due to the fact that at that time the genus *Neoclitocybe*, with truly decurrent lamellae, was not yet known.

Much closer to *Marasmiellus* in the present definition are *Neoclitocybe* and *Micromphale*. These genera are characterized by, in the case of *Neoclitocybe*, decurrent lamellae and a clitocyboid to omphaliod habit, in the case of *Micromphale* by a strong development of gelatinous trama in and/or below the epicutis. Since some Marasmielli have eventually subdecurrent or even slightly decurrent lamellae (although usually not consistently so) and others have gelatinous layers (although generally in a somewhat lower subcuticular or supralamellar layer of the trama), it is necessary to explain the delimitation of the three genera fully.

*Neoclitocybe* may or may not have a distinct *Rameales*-structure and may or may not have a distinct basal mycelium. It has, however, always decidedly decurrent lamellae or at least never less than arcuate-subdecurrent ones, their stipe is not more than occasionally eccentric, usually quite central. The spores are within the range of *Marasmiellus* spores, but often excessively small. There are no gelatinized tromal zones as far as we now know. Under these circumstances, the only case in which difficulties in separation could occur are in the species with eccentric stipe in *Neoclitocybe* on one hand and the section *Marasmiellus* of *Marasmiellus* on the other, where non-insititious stipe base and absence of a true *Rameales*-structure frequently occur. This would tend to single out the following taxa as transitional: *Neoclitocybe sublateralis* Sing. and *Marasmiellus* subsection *Inodermini* on the other. Since there is no sharp dividing line between the species of subsection *Inodermei* with occasionally subdecurrent lamellae and those with strictly adnexed, rounded or adnate lamellae, and the fungi entering this subsection are all extremely closely related to each other, it appears to be the best solution to make the decidedly decurrent lamellae in eccentrically stipitate forms the decisive character - and one in line with the original definition of the genus *Neoclitocybe* - so that *Neoclitocybe sublateralis* is, after all, better classified in *Marasmiellus* than in *Neoclitocybe* and thus the respective transfer has been made.

This group is also the group where *Marasmiellus* seemingly comes closest to *Hemimycena*. But in this genus the stipe appears to be normally central and even the species with decidedly decurrent lamellae are always pigment-less or almost so, and the base of the stipe almost constantly showing a distinct basal mycelium. Thus, if we limit the Marasmielli with centrally attached stipe and white pileus and stipe to those with insititious or subinsititious base (unless, of course, they have characteristics unknown in *Hemimycena*, like setoid hairs or absence of clamp connections or a typical *Rameales*-structure), there cannot be any difficulty in delimiting *Hemimycena* from *Marasmiellus* as well as *Neoclitocybe*. If in totally white species non-fusoid basidia and presence of a distinct basal mycelium are not correlated, or basidioles are mostly fusoid and the basal mycelium is only poorly developed, the species belongs to *Marasmiellus*. Species with a sily veil or volva belong in *Marasmiellus*. Probably, once the tramal structure of all Hemimycenae is more fully known, the differentiation between the two genera will be even easier, considering that most typical Hemimycenas have a number of voluminous (*Mycena*-type) or broad and strongly elongated cells in the trama, mixed with normal filamentous ones, and this structure has caused Corner (1966) to name the respective tramal structure "sarcodimitic".

As for *Micromphale*, the absence of any trace of *Rameales*-structure in the epicutis of the pileus combined with a gelatinous layer in the pileus and/or the presence of (and frequently the development of carpophores from) dark rhizomorphs, should be a sufficient combination of characters to exclude all confusion with *Marasmiellus*.

*Cymatella* differs in the complete absence of a hymenophore. Such a condition occurs extraordinarily rarely in *Marasmiellus*, and then only as an exceptional condition of one or another carpophore in a population, and even so, in species completely unrelated to *Cymatella*.

As for *Pterospora*, it has become clear to me (Singer 1975) that the type species of that genus belongs in *Marasmiellus*. The "pterosporous" species are so closely related to the bulge-less spores in both *Marasmiellus* and *Campanella* (and often mixed with bulge-less spores in some species) that *Pterospora* sensu Horak (1984) must be considered highly artificial because of the obvious overestimation of a single specific character. *Pterospora*-spores, by the way, exist also in other tricholomataceous genera.

*State of knowledge:* The genus has been monographed for the Neotropics and much valuable work has been published by Pegler on the Australian, Africa and Asiatic species. All European species can now be determined with Moser's or Kühner & Romagnesi's keys if more recent studies are also taken into consideration especially Singer, *Nova Hedwigia Beih.* 44, 1973. We admit now 162 well known species. See pl. 58, 2.

*Practical importance:* Diseases of sugar cane, corn plants, beech grass and lawn grasses, banana, various cultivated palms (such as *Cocos nucifera* and *Elaeis guineensis*) have been caused by pathogenic species of *Marasmiellus*; some species

grow on the bark of living trees and seem to be only mildly parasitic; this includes important crop plants such as *Coffea*, *Hevea*.

## SPECIES

Sect. 1. *CANDIDI* (Bat.) Sing. (1961). No *Rameales*-structure or this structure disappearing in age; spores large ( $>10.4 \mu\text{m}$  long); setoid cells absent; stipe usually tending to grayish at the base; pigments usually scanty or absent in the pileus.

*Type species:* *Marasmius candidus* (Bolt. ex) Fr. = *Marasmiellus albuscorticis* (Secr.) Sing.

*M. albofuscus* (Berk. & Curt.) Sing.; *M. subnigricans* (Murr.) Sing.; *M. albuscorticis* (Secr.) Sing.; *M. coilobasis* (Berk.) Sing.; *M. volvatus* Sing.

Sect. 2. *DEALBATI* Sing. (1973). Spores smaller than in preceding section and stipe generally not tending to gray. Pigmented and non-pigmented species.

*Type species:* *M. dealbatus* Berk. & Curt.

Subsection *Dealbatini* Sing. (1973). Pileus quite or almost pigment-less.

*Type species:* *M. dealbatus* Berk. & Curt.

*M. dealbatus* (Berk. & Curt.) Sing.; *M. subgraminis* (Murr.) Sing.; *M. stenophyllus* (Mont.) Sing.; *M. synodicus* (Kunze apud Fr.) Sing.; *M. carneopallidus* (Pouz.) Sing.; *M. vaillantii* (Pers. ex Fr.) Sing.; apparently also *M. setulosipes* (Murr.) Dennis sensu Pegler 1977 (but quite different from *Hemimycena setulosipes* (Murr.) Sing. sensu Murrill).

Subsection *Quercini* Sing. (1973). Pileus distinctly pigmented, not white.

*Type species:* *M. quercinus* Sing.

*M. minutus* Sing.; *M. alneus* Sing.; *M. paraensis* Sing.; *M. napoensis* Sing.; *M. amphicystis* Sing.; *M. hondurensis* (Murr.) Sing.; *M. mesosporus* Sing.; *M. ramorum* Sing.; *M. corynophloeus* Sing.; *M. angustispermus* Sing.; *M. quercinus* Sing.; *M. xerophyticus* Sing.; *M. dendroegrus* Sing.; *M. enodis* Sing.; *M. dryogeton* Sing.; *M. aurantiorufescens* Sing.; *M. subolivaceomelleus* Sing.; *M. baeosporus* Sing.; *M. pandoensis* Sing.; *M. nothofagineus* Sing.; apparently also *M. pachycraspedum* Noordeloos.

Sect. 3. *STENOPHYLLOIDES* Sing. (1973). Much like section 1, but with setoid hairs with pigmented walls; epicutis with or without *Rameales*-structure.

*Type species:* *M. stenophylloides* (Dennis) Dennis.

*M. peckii* (Murr.) Sing.; *M. crinipelloides* Sing.; *M. atrosetosus* Dennis; *M. echinocephalus* Sing.; *M. tenerrimus* (Berk. & Curt.) Sing.; *M. stenophylloides* (Dennis) Dennis; *M. setulosus* (Joss. & Smith) Sing.; *M. elongatisporus* Sing.

Sect. 4. *TETRACHROI* Sing. (1973). *Rameales*-structure on pileus present or

absent; carpophores strongly pigmented; spores up to 8.7  $\mu\text{m}$  long; stipe at its base distinctly and often abruptly attenuated.

*Type species: M. tetrachrous* (Sing.) Sing.

*M. tetrachrous* (Sing.) Sing.; *M. sprucei* (Berk.) Sing.

Sect. 5. *TRICOLORES* Sing. (1973). *Rameales*-structure on pileus present; spores generally large ( $>10.4 \mu\text{m}$ ; pileus usually white, cream, gray or greenish; setoid hairs and abruptly attenuated stipe-base absent, but the latter often tending to caesious or gray. Hymenial cystidia none or inconspicuous.

*Type species: M. tricolor* (A. & S. ex Fr.) Sing.

*M. caesioater* (Speg.) Sing.; *M. tricolor* (A. & S. ex Fr.) Sing. (*Marasmius graminis* Murr.; *M. pruinatus* Rea; *M. languidus* (Lasch) Fr.; *M. vialis* Peck), with several varieties; *M. berkeleyi* Sing.; *M. cubensis* Berk. & Curt.) Sing.; *M. caracassensis* Dennis ex Sing.; *M. caespitosa* (Pat.) Sing. (*M. trabutii* (Maire) Sing.

Sect. 6. *RAMEALES* (Lange "Rameali") Sing. (1951). Pileus not pigmented (and then spores up to 10.5  $\mu\text{m}$  long) or pigmented, with a distinct *Rameales*-structure; stipe not abruptly attenuated at the base and no setoid hairs on the covering layers. Trama of the pileus without gelatinous zones or pockets; spores not with an asymmetrical bulb nor triangular or cross-shaped.

*Type species: M. ramealis* (Bull. ex Fr.) Sing.

Subsection *Opacini* Sing. (1972). Pileus generally white or whitish (primordia often deeper colored or pale colored in wet specimens, fading to white).

*Type species: M. opacus* (Berk. & Curt.) Sing.

*M. nivosus* (Berk.) Sing.; *M. petiolorum* (Berk. & Curt.) Sing.; *M. eburneus* (Theissen) Sing.; *M. stenosporus* Sing.; *M. bermudensis* (Berk.) Sing.; *M. confertifolius* Sing.; *M. caatingensis* (Berk.) Sing.; *M. omphalodes* (Berk.) Sing.; *M. albobrunnescens* Sing.; *M. opacus* (Berk. & Curt.) Sing.; *M. chilensis* (Speg.) Sing.; *M. humillimus* (Quél.) Sing. Here perhaps *M. cocophilus* Pegler, *M. ugandensis* Pegler, and *M. pluvius* Redhead.

Subsection *Umbilicatini* Sing. (1973). Pileus pigmented; stipe with filamentous, thick-walled, more or less brownish-walled hairs like those of *Crinipellis*, but not pseudoamyloid, rather long (often up to and over 100  $\mu\text{m}$ ) and always entire.

*Type species: M. umbilicatus* Sing.

*M. laurifoliae* Sing.; *M. foliorum* Sing.; *M. androsaceiformis* Sing.; *M. umbilicatus* Sing.; *M. peullensis* Sing.; *M. papillifer* Sing.; *M. omphalomorphus* Sing. Probably here *M. hirtellus* (Berk. & Br.) Pegler (vix *Collybia hirtella* sensu Dennis).

Subsection *Pseudoconidiophori* (Sing.) Sing. (1973). (Hemimycena sect. *Pseudoconidiophori* Sing. 1943). Diverticula globulose-conidia-like in epicutis and cheilocystidia. Otherwise like the Opacini or Ramealini. Lignicolous, in Asia.

*Type and only species: M. pseudoconidiophorus* (Sing.) Sing.

**Subsection Ramealini** Sing. Stipe covering not with Crinipellis-like hairs; pileus not white; edge of lamellae generally not discolored as in the subsequent subsection.

*Type species:* *M. ramealis* (Bull. ex Fr.) Sing.

*M. subingratus* (Dennis) Dennis; *M. osmophorus* Dennis; *M. viridifuscus* (Berk. & Curt.) Sing.; *M. incarnatipallens* Sing.; *M. roseotinctus* Pegler; *M. tener* Sing.; *M. yalae* Sing.; *M. pygmaeus* (Rick) Sing.; *M. rugulosus* (Berk. & Curt.) Sing.; with ssp. *ricardii* Sing.; *M. daguae* Sing.; *M. aquilus* Sing.; *M. iguazuensis* Sing.; *M. umbonifer* Sing.; *M. stenocystis* Sing.; *M. brasiliensis* (Berk. & Mont.) Sing.; *M. albifolius* Sing.; *M. incrustatus* Sing.; *M. filopes* (Peck) Redhead; *M. gomezpompae* Sing.; *M. subramealis* Sing. in Sing. & Digilio; *M. ramealis* (Bull. ex Fr.) Sing. (both last species with several varieties); *M. cystidiosus* Sing.; *M. antarcticus* Sing.

**Subsection Brunneomarginatini** Sing. (1973). Edge of lamellae discolored (pale tawny from cheilocystidia); spores narrow ( $Q = 3$  or more); pileus not white.

*Type species:* *M. brunneomarginatus* Sing.

*M. bonaerensis* (Speg.) Sing.; *M. brunneomarginatus* Sing.; *M. polyphyllus* Sing.; *M. papillatomarginatus* Sing.; *M. perangustisperatus* Sing.

Sect. 7. **DEFIBULATI** Sing. (1973). Differs from all other sections in the absence of clamp connetions.

*Type species:* *M. defibulatus* Sing.

**Subsection Defibulatini** Sing. (1972) Pileus mainly white.

*Type species:* *M. defibulatus* Sing.

*M. defibulatus* Sing.; *M. bisporiger* Sing.; *M. pseudoparaphysatus* Sing.; obviously also *M. pusillimus* Redhead & Liu.

**Subsection Subcoracini** Sing. (1972) Pileus strongly pigmented.

*Type species:* *M. subcoracinus* (Berk. & Curt.) Sing.

*M. nubigenus* Sing.; *M. picipes* (Murr.) Sing.; *M. aporpopeptus* Sing.; *M. columbianus* Sing.; *M. subcoracinus* (Berk. & Curt.) Sing. with ssp. *montanus* Sing.

Sect. 8. **MARASMIELLUS**. Habit pleurotoid; clamp connections present; trama not gelatinized; spores not asymmetrically extended, not tetrahedric or cross-shaped.

*Type species:* *M. juniperinus* Murr.

**Subsection Sphaerosporini** Sing. (1973). Spores characteristically broad.

*Type species:* *M. sphaerosporus* Sing.

*M. gigantosporus* Sing.; *M. rhodophyllus* Sing.; *M. trichodermialis* Sing.; *M. sphaerosporus* Sing.; *M. parlatorei* Sing.; *M. guzmanii* Sing.; *M. guadalupeensis* (Pat.) Sing. (Xerotus, Pat.; Nothopanus, Sing. 1944).

Subsection *Inodermini* Sing. (1973). Pigment violet-purple or nearly absent in pileus; odor not of garlic. Spores not particularly broad, but ellipsoid to oblong, cylindric or fusoid. Lamellae unicolor.

Type species: *M. inoderma* (Berk.) Sing.

*M. sanctaemarthae* Sing.; *M. purpureus* (Berk. & Curt.) Murr.; *M. vinosus* Sing. in Sing. & Digilio; *M. troyanus* (Murr.) Dennis; *M. pernambucensis* Sing.; *M. semiustus* (Berk. & Curt.) Sing. with var. *semiustus*, var. *sabali* (Berk.) Sing. and var. *abortivus* Sing.; *M. musacearum* Sing.; *M. inoderma* (Berk.) Sing.; *M. inodermatoides* Sing.; *M. ambiguus* Sing.; *M. inconspicuus* Murr.; *M. segregabilis* Sing.; *M. thaxteri* Sing.; *M. epochnous* (Berk. & Curt. in Berk. & Br.) Sing.; *M. panamensis* Sing.; *M. tropicalis* (Speg.) Sing.; *M. schiffneri* (Bres.) Sing.; *M. concolor* (Berk. & Curt.) Sing.; *M. microscopicus* (Speg.) Sing.; *M. sublateralis* (Sing.) Sing.; *M. gossypinulus* (Speg.) Sing.; *M. couleu* Sing.; *M. paspali* (Petch) Sing.; *M. cataphes* (Berk.) Sing. probably here: *M. calami* (Petch) Sing. and *M. scandens* (Mass.) Dennis & Reid (both at any rate in sect. *Marasmiellus*). According to Reid also *M. contrarius* (Kalchbr.) Reid.

Subsection *Bolivarianini* Sing. (1972). Edge of lamellae discolored.

Type species: *M. bolivarianus* Sing.

*M. bolivarianus* Sing.; *M. osorniensis* Sing.

Subsection *Gilvini* Sing. (1973). Pileus with at least a zone of well pigmented surface layer; spores not particularly broad; lamellae not distinctly discolored; odor sometimes alliaceous.

Type species: *M. gilvus* (Pat.) Sing.

*M. alliodorus* (Bertero ex Mont.) Sing. ex Sing.; *M. ignobilis* (Berk. & Br.) Sing.; *M. luteus* (Dennis) Sing.; *M. idroboi* Sing.; *M. cnacopolius* Sing.; *M. oligocinsulae* Murr.; *M. juniperinus* Murr.; *M. laschiopsis* Sing. apud Dennis; *M. platyhyses* Sing.; *M. misionensis* Sing.; *M. alvaradoi* Sing.; *M. orinocensis* Sing.; *M. riberaltensis* Sing.; *M. curtipes* (Murr.) Sing.; *M. gilvus* (Pat.) Sing. (with several varieties). According to Reid also *M. clusilis* (Kalchbr.) Reid and *M. radiatimplicatus* (Kalchbr.) Reid (but the latter may be closer to *Marasmius* sect. *Fusicystides*. Here apparently also *A. amygdalosporus* Pegler and *M. sinensis* Redhead & Liu.

Sect. 9 *DISTANTIFOLII* Sing. (1961). Habit pleurotoid; gelatinized zone(s) or pockets in the pileus trama obvious; spores not asymmetric.

Type species. *M. distantifolius* (Murr.) Sing.

*M. cinereus* Sing.; *M. devenulatus* Sing.; *M. distantifolius* (Murr.) Sing.; *M. merilius* (Bertero) Sing.; *M. afer* Pegler.

Section 10. *NIGRIPEDES* Sing. (1973). Habit collybioid or pleurotoid; gelatinized zone(s) or pockets in the trama of the pileus present; spores tending to be asymmetric in the sense that they have bulges or a bulge so that they appear in certain

positions triangular or cross-shaped; clamp connections present; *Rameales*-structure present; carpophores often tending to be or become gray, caesious, green, black, blue, at least in the lower part of the stipe; spores medium sized (about 5-10  $\mu\text{m}$  long).

*Type species: M. nigripes* (Schwein.) Sing.

*M. nigripes* (Schwein.) Sing. with several varieties including var. *subcinereus* (Berk. & Br.) Pegler and *Pterospora atrocyanea* Métrod; *M. reductus* Sing.; probably close to the latter: *M. bambusicola* (Corner) Redhead (Leptoglossum, Corner)

## 59. MICROMPHALE Nees ex S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 621. 1821; em. Sing. (non sensu Murr.).

*Type species: M. venosum* (Pers. ex) S.F. Gray [= *M. foetidum* (Sow. ex Fr.) Sing.].

*Syn.: Heliomyces* Lév. sensu Sing. (1936), R. Maire (1937) non sensu originali (see *Marasmius*).

*Characters:* Habit of the carpophores strictly marasmoid; pigment frequently intraparietal and incrusting the walls of certain hyphae; epicutis of the pileus (which is often striate or sulcate, often umbilicate, usually well-colored, thin) little differentiated, with smooth, filamentous, repent hyphae which are either parallel with each other or irregularly interwoven; often imbedded in a mucous mass as are frequently also the hyphae of the context, or else interrupted with air spaces; lamellae adnate to decurrent, subclose to distant; spore print white; spores hyaline, thin-walled, smooth, nonamyloid, ellipsoid-oblong or fusoid, or short-ellipsoid; cheilocystidia not very striking, basidiomorphous or in the shape of the basidioles (fusoid), if clavate, often with nodulose or ramosely appendiculate apices and their lower portions and the adjacent subhymenium incrusted by pigment; stipe deep fuscous black, or black, or somehow deep colored, pilose, pruinose or glabrous, insititious, central, more rarely eccentric or lateral; black rhizomorphs sometimes well developed; context tough and reviving; trama of carpophores inamyloid, often partly gelatinized or with air-spaces between the strands of hyphae; all hyphae with clamp connections; odor frequently fetid. On branches and logs, also on conifer needles, petioles and herbaceous stems and on culms.

*Development of the carpophores:* Paravelangiocarpous according to Reijnders in *M. perforans*, apparently gymnocarpous in *M. austrochilensis*.

*Area:* Almost cosmopolitan (certainly absent in Antarctica).

*Limits:* If the dark rhizomorphs are present (and some or all carpophores rise from them) while the epicutis is not a *Rameales*-structure nor hymeniform and the trama is inamyloid, the species is sufficiently related to the type species of *Micromphale* to be inserted there. If the cuticular layer or a tramal layer is strongly gelatinized, and there is no *Rameales*-structure on the pileus, which is pigmented, the respective species is also to be considered as belonging in *Micromphale*. With these criteria, a sharp delimitation between *Marasmiellus* and *Micromphale* is easily established.

Only *M. macrosporum* appears to be somewhat intermediate between *Marasmiellus* sect. *Candidi* and *Micromphale*, but since there are neither cystidia nor dermatocystidia present and the mediostratum appears slightly gelatinized, the species is here inserted in *Micromphale*.

Kühner (180, p. 158) is puzzled by the fact that three European species with alliaceous odor and belonging in *Marasmius* according to Kühner & Romagnesi, should be placed in three different genera in our classification. (*Marasmius*, *Collybia*, and *Micromphale*). If the world flora is considered, we find that in the *Collybieae* and *Marasmieae* many more species with this odor exist, including in *Marasmiellus* and even in *Clavaria*. A specific odor is rarely restricted to a single genus.

*Micromphale* differs from *Campanella* in the configuration of the hymenophore which is strictly lamellate and only sometimes slightly intervenose, and the different structure of the epicutis which is never a *Rameales*-structure nor asterostromelloid in *Micromphale*; pleurocystidia are often found in *Campanella* where they may even be metuloid and if thin-walled, often capitate.

Black rhizomorphs are often found in the *Marasmieae* but there the epicutis has a completely different structure, and gelatinous layers are absent in the trama. *Armillariella* cannot be confused with *Micromphale* since all species of *Armillariella* lack clamp connections in the trama hyphae and the habit is totally different. Only one species, possibly belonging in *Micromphale* has been described as clamp-less, viz. *M. inodorum* Dennis which I have not studied (except for a colored sketch, now published in Dennis, Fungus flora of Venezuela, plate 7, fig. 15, 1970). The position of this species remains ambiguous.

The genus *Heliomyces* is characterized in a way to suggest that it coincides with what we now call *Micromphale*. In fact, Singer and later Maire decided in favor of the generic name *Heliomyces*, in order to avoid the creation of a new generic name. However, the typical species of *Heliomyces* in the original sense have all the anatomical and chemical characters of *Marasmius*.

*State of knowledge:* Ten species are here recognized as belonging in *Micromphale*.

*Practical importance:* It is possible that in addition to a *Marasmius*, a *Micromphale* is also involved in the so-called Horse-hair Disease in Malaya.

## SPECIES

Sect. 1. *RHIZOMORPHIGENA* Sing. (1948). Characters much like those of the section *Rameales* of *Marasmiellus* but epicuticular hyphae (though strongly incrusted by the pigment) nearly non-diverticulate, irregularly interlaced, weakly or not gelatinized; stipe black, hirsute-pilose or glabrous, in most cases directly continuing into black, branching, horsehair-like rhizomorphs; cheilocystidia nodulose or somewhat appendiculate-branched at the apex, otherwise basidiomorphous; pileus often eccentric.

*Type species: M. westii* (Murr.) Sing.

*M. brevipes* (Berk. & Rav.) Sing. apud Dennis [Marasmius, Berk. & Rav.; *M. westii* (Murr.) Sing.; Marasmius, Murr.]; *M. tomentosum* Sing.

Sect. 2. *PERFORANTIA* Sing. (1948). Characters of the preceding section but stipe subpruinose or tomentose, the black rhizomorphs little or less developed than in the preceding section, and the stipes rarely rising from them; hyphae of the upper stratum of the pileus generally gelatinizing in the course of development; trama beneath the cortical layer not gelatinized; cheilocystidia indistinct or distinct; stipe generally central, dark colored, and growing on fallen needles, leaves or wood.

*Type species: M. perforans* (Hofm. ex Fr.) Sing.

*M. perforans* (Hofm. ex Fr.) Sing.; *M. separatum* Sing.; *M. occidentale* Sing.

Sect. 3. *MICROMPHALE*. A gelatinous or subgelatinous layer present beneath the non-gelatinized epicuticular layer, either in the trama of the pileus or in the mediostratum of the lamellae; stipe lateral, eccentric or central, not rising from but sometimes accompanied by black rhizomorphs, if central often relatively short, not glabrous; pileus generally distinctly transparently striate or sulcate. Mostly lignicolous, more rarely on *Eucryphia* leaves or *Chusquea* culms.

*Type species: M. foetidum* (Sow. ex Fr.) Sing. (*M. venosum* (Pers. ex) S.F. Gray).

*M. foetidum* (Sow. ex Fr.) Sing.; *M. austrochilense* Sing.; *M. subavellaneum* (Murr.) Dennis; *M. griseum* Sing.; *M. macrosporum* Sing.; possibly also *M. inodorum* Dennis.

## 60. CAMPANELLA Henn.

*Engl. Bot. Jahrb. 22(1): 95. 1895.*

*Type species: Campanella buettneri* Henn.

*Syn.: Laschia* Pat. *Essai tax. Hymen.*, p. 129. 1900, non Fr., nec Jungh.

*Laschia* sect. *Campanella* (Henn.) Pat., *l.c.*

*Laschia* sect. *Eulaschia* Pat., *Journ. de Bot.* 1: 231. 1887.

*Laschia* sect. *Laschiella* Henn., in Engl. & Prantl, *Nat. Pflanzenfam.* I, 1\*\*: 186. 1900.

*Characters:* Habit pleurotoid; trama at least partly strongly gelatinized, inamyloid with clamp connections; epicuticular zone of pileus an imperfect or well developed *Rameales*-structure or asterostromelloid layer (dichophyses); metuloids or other cystidia sometimes present; spores ellipsoid, subglobose, inamyloid, acyanophilic, thin-walled, sometimes with a bulge on the outer side, or obscurely angular or otherwise irregular, but not stellate, smooth; hymenophore strongly anastomosing, mostly at equal height as the radiating lamellae so that it appears almost poroid-alveolate much like that of *Polyporus dermoporus* Pers. (= *Favolus brasiliensis* Fr.) but narrower usually some lower ridges or anastomoses present and these generally less regular; carpophores to 30 mm diam. and almost transparent, with or without a

(very eccentric to lateral) stipe or a dorsal pseudostipe; on various plant stems and wood.

*Development of the carpophores:* Unknown.

*Area:* Generally tropical and subtropical, tropical-montane, and one species reaching northern Florida, two Europe and three the Southern Andes (*Nothofagus* region).

*Limits:* The delimitation of the genus does not present difficulties; it has been discussed under similar genera (e.gr. *Micromphale*).

*State of knowledge:* The species now known and here admitted (about 30) are well known except for their development. See Pl. 57.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *CAMPANELLA*. Metuloids absent.

*Type species:* *C. buettneri* Henn.

Subsection *Gigantosporae* Sing. (1975). Spores voluminous (in the type species 11-15.5 × 9.5-12 µm); cystidia diverticulate.

*Type species* and only known species: *C. gigantospora* Sing.

Subsection *Elongatisporae* Sing. (1975). Spores elongate (longer than 10 µm, up to 5.3 µm broad); pileus white or yellow, not green or greening.

*Type species:* *C. elongatispora* Sing.

*C. elongatispora* Sing.; *C. agaricina* (Mont.) Lloyd.

Subsection *Aerugineae* Sing. (1975). Spores neither consistently elongate nor minute (5.5-10.5 × 3-6 µm), usually variable in shape; carpophores green or glaucous or becoming so.

*Type species:* *C. aeruginea* Sing.

*C. aeruginea* Sing.; *C. aberrans* Sing.; *C. merulina* (Pers.) Sing. (*Agaricus*, Pers., non *C. merulina* (Berk. & Curt.) Sing., comb. inval. Art 33.2; 64.1); *C. caesia* Romagnesi (unless too close to the preceding species).

Subsection *Campanella* (Albae Sing. 1975). Spores >6.5 µm, not elongated with or without asymmetrical bulges, pigments none or grayish to caesious (not glaucous), or pale buff to brownish.

*Type species:* *C. alba* (Berk. & Curt.) Sing.

*C. castaneipes* Sing.; *C. tenuitunicata* Sing.; *C. buettneri* Henn.; *C. alba* (Berk. & Curt.) Sing.; *C. cucullata* (Jungh.) Lloyd; *C. witteana* Sing.; *C. peullensis* Sing.; *C. subdendrophora* Redhead; *C. austrochilensis* Sing.; *C. inquilina* Romagnesi in

Redhead (*C. europaea* Sing. ad int. 1975; *Leptoglossum conchatum* "Velen." sensu Kühner & Romagnesi).

Subsection *Floridanae* Sing. (1975). Spores short ellipsoid to subglobose, to 6.5  $\mu\text{m}$  long, or, if longer, rising from bisporous basidia.

*Type species:* *C. floridana* Sing.

*C. podocarpi* Sing.; *C. floridana* Sing.; *C. alnetorum* Sing.; *C. caerulescens* (Berk. & Curt.) Sing.; *C. boninensis* (S. Ito & Imai) Parmasto.

Sect. 2. *DIPLOCYSTIDES* Sing. (1975). Metuloids present, often mixed in with thin-walled and branched elements.

*Type species:* *C. diplocystis* Sing.

*C. stipitata* (Sing.) Sing.; *C. aequatorialis* Sing.; *C. simulans* (Pat.) Sing.; *C. dendrophora* Sing.; *C. capensis* (Berk.) Reid.; *M. diplocystis* Sing.

Other species of *Campanella* (all sect. *Campanella*): *C. eberhardtii* (Pat.) Sing.; *Dictyotus castaneus* Peck (acc. to Redhead in litt.); *C. purpureobrunnea* Petch; probably also *Marasmiellus filocystis* Redhead & Liu.

#### Reduced series: 61. CYMATELLA Pat.

*Bull. Soc. Myc. Fr.* 15: 193. 1889.

*Type species:* *C. marasmiooides* (B. & C.) Pat.

*Characters:* Habit like that of *Marasmiellus* sect. *Marasmiellus*; pileus small, glabrous, thin, with an epicutis of diverticulate hyphae in the manner of the *Marasmiellus*, sect. *Rameales* (Rameales-structure); hymenophore none; hymenial surface smooth, or almost so, cystidia none; spores hyaline, thin-walled, inamyloid, smooth, cylindric to obovate, medium sized (5.5-9  $\pm$  2-3.7  $\mu\text{m}$ ); basidioles fusoid; stipe rather tough, thin and dark colored, not shining, always well developed but usually eccentric to lateral; trama of the pileus consisting of thin- to moderately thin-walled hyphae, often incrusted by pigment, especially in the hypodermium, filamentous, with clamp connections, only in 2-spored forms clampless, inamyloid. The hymenial surface is directed towards the ground (downwards). Trama monomitic and not gelatinized. On rotting wood, twigs, and dead ferns.

*Development of the carpophores:* Unknown.

*Area:* Neotropics.

*Limits:* This differs from *Marasmiellus* in the absence of lamellae. As for *Skeperiella*, see key. *Mniopetalum* and *Calyptella* are more cyphelloid and stipe-less. *Phaeodepas* is clamp-less.

*State of knowledge:* All five species have been studied by the author and compared with the types.

*Practical importance:* Unknown.

## SPECIES

*C. minima* Pat.; *C. marasmoides* (Berk. & Curt.) Pat. (*Craterellus*, B. & C.); *C. pulverulenta* (Berk. & Curt.) Pat. (*Craterellus*, B. & C.); *C. defibulata* Sing; also "Cymatellopsis" *ibriana* Parmasto in sched.

### Reduced series: 62. **SKEPPERIELLA** Pilát

*Bull. Soc. Myc. Fr.* 43: 56. 1927.

*Type species:* *Craterellus spathularius* Berk. & Curt.

*Characters:* Habit of the carpophores spathuloid-spoon-shaped with a strictly lateral true stipe which is solid and insititious, often white but sometimes somewhat darkening below; hymenial surface smooth, but sometimes some carpophores of a population with rudimentary to rather well developed lamelliform hymenophore, but mature specimens with smooth hymenial surface present; cystidia mostly present, but often easily collapsing and few, at times restricted to the rim of the pileus which is white and subtomentose-pruinate, but on drying cream to pale buff-pink or sordid tan in most collections, and glabrescent; spores hyaline, smooth, thin-walled, inamyloid, ellipsoid (5.3)-6.7-8.3 ± (3.5)-4-6.7  $\mu\text{m}$  not narrower and not longer; basidia normal; basidioles fusiform; trama of the pileus hyaline, monomitic, consisting of thin- to firm-walled hyphae with clamp connections and without pigment, not gelatinized, inamyloid. Epicutis of the pileus and/or the stipe with a weak to distinct Rameales-structure; below it hyphae subparallel with each other, inamyloid in the stipe; outer layer below hymenium with a subhymenium of very small but not consistently subcellular elements, below the subhymenium a strongly interwoven hymenopodium. On wood, but also on rocks, often associated with algae (*Nostoc*).

*Development of the carpophores:* Unknown.

*Area:* From the neotropics south to the Buenos Aires region, perhaps more widely distributed.

*Limits:* This genus has been compared and perhaps confused with *Rimbachia* (but compare under that genus) and *Cymatella*, which is closest and from which it differs in habit, spore shape, and shorter stipe, the latter less pigmented. *Marasmiellus* differs in habit and does not form sporulating carpophores without hymenophore.

*State of knowledge:* Only two species are well known. See Singer (1965).

*Practical importance:* Unknown.

## SPECIES

*S. spathularia* (Berk. & Curt.) Pilát; *S. populi* Sing.

*Persoonia* 2: 332. 1962.

*Type species:* *M. globisporum* Donk.

*Characters:* Pigment-less white membranous carpophores attached laterally or in some area of the sterile surface, not or inconsistently cup-shaped, and not normally stipitate or pseudostipitate or, if pseudostipitate, only shortly and inconstantly so, with lobed, irregular outline when mature; spores hyaline, smooth, thin-walled, guttiform, subglobose or ellipsoid (between 5.5 and 10  $\mu\text{m}$  long and between 4 and 7  $\mu\text{m}$  broad), inamyloid; basidia normal, 2- or 4-spored; trama with clamp connections, not gelatinized, strictly monomitic, most hyphae filamentous, some inflated towards the sterile surface, the latter (epicutis) little differentiated but often with a few nodules, or erect branchlets or with wavy outline and in places intricately interlaced, at times forming a weak Rameales-structure or frequent forked hyphal ends or small isodiametric outgrowths; all hyphae inamyloid. The hymenial surface directed downwards. Generally growing on living Bryophyta (but also passing over onto living Pteridophyta and angiosperm leaves and twigs).

*Development of the carpophores:* Unknown. As for cultural characters see Kühner in Kühner & Romagnesi, *Soc. Nat. d'Oyonnax* 8: 78. 1954.

*Area:* In Europe and Asia (Himalaya), in the tropical-montane zone of Southern South America south to South Chile, perhaps with a wider distribution.

*Limits:* The shallowly cupuliform to irregular-membranaceous carpophores without any pigment, the relatively broad to subglobose spores, and the habitat are characteristic. *Mniopetalum* differs from the two preceding genera in the absence of a stipe, a less developed Rameales-structure and the habitat. Lamellate individuals should not be confused with *Cheimonophyllum* and *Marasmiellus* sect. *Marasmiellus* which are consistently lamellate and not growing on living moss thalli. The habitat has induced some mycologists to think that the genus *Mniopetalum* might be combined with *Leptoglossum* but the two genera are not closely related and *Mniopetalum* can always easily be distinguished by the lack of incrusting pigment. *Pleurotellus* differs in colored spore print and absence of clamp connections. Kühner (1980) combines *Mniopetalum* and *Pleurocybella* in a single subgenus of *Nothopanus*. But *Nothopanus* is a *Pleurotus* sect. *Pleurotus*. *Mniocephalum* differs from *Pleurocybella* in habit (much thinner, with poorly and slowly, often not at all developing, never crowded lamellae) and habitat. Although the Rameales-structure is not always distinctly developed in *Mniopetalum*, the two genera have nothing but the lack of pigments and the lack of a stipe in common.

*State of knowledge:* Four species are well known.

*Practical importance:* Unknown.

## SPECIES

*M. arachnoidea* (Peck) Sing.\*; *M. bryophilum* (Pers. ex Fr.) Donk; *M. bisporum* Sing.; *M. megalosporum* Sing. (*Rimbachia neckerae* ssp. *megalospora* (Sing.) Redhead); according to Redhead's data also *Cyphella muscicola* var. *neckerae* (Fr.) Fr. = *Leptoglossum candidum* Reid and *Rimbachia paludosa* Redhead; possibly *Leptoglossum omnivorum* Agerer\*\*.

### Reduced series: 64. CYPHELLA Fr.

*Syst. Myc.* 2: 201. 1823.

*Type species:* *Cyphella digitalis* (A. & S. ex Pers.) Fr.

*Characters:* Habit cyphelloid, pendulous, small, often centrally or eccentrically attached by a pseudostipe which is short, with smooth, concave hymenial surface; pigment present, intraparietal and often incrusting; cortical layer of repent, ascendant and erect hyphal ends, brown, thin- to thick-walled, often subcapitulate, forming a trichodermium, but at the rim of the carpophores passing into cystidiiform elements which form a transition to the hymenial layer; no Rameales structure present; trama monomitic, of filamentous, inamyloid hyphae with clamp connections, not gelatinized; spores characteristically large (up to and above 17 µm), globose, hyaline, some somewhat thick-walled, smooth, inamyloid. On (coniferous) wood (mostly *Abies* in the type species).

*Development of the carpophores:* Unknown.

*Area:* North-temperate zone.

*Limits:* *Cyphella* is not as Donk believed an *Aleurodiscus* (Favolaschiaceae) which differs in structure and amyloidity of the spore wall which is typically not smooth, but seems to be close to *Marasmiellus* sect. *Marasmiellus* and *Cymatella* (which differs in the presence of a Rameales-structure and a stipe). The large globose spores have caused most mycologists to disregard the agaricoid affinities of this genus, but *Marasmiellus gigantosporus* has all the characteristics of a good *Marasmiellus* (although the Rameales-structure is rather poor in the trichodermium of the epicutis) and has spores 13-22.5 × 13-22 µm, with thin to thickish wall (up to 1.2 µm); here, the stipe is lateral, the lamellae few, and most hyphae have pigment incrustation. When this species was discovered there remained no doubt that *Cyphella* is not related to any Aphyllophorales but belongs in the reduced series of the *Collybieae*.

Once admitted to the Agaricales, it is clear that *Cyphella* is not only close to *Marasmiellus* and *Cymatella*, but also to *Phaeodepas*, *Calyptella*, and *Skepperiella*. It can easily be distinguished from these three genera by the key characters.

*State of knowledge:* Only one species is known.

\*c.n. (*Cyphella arachnoidea* Peck, *Rep. N.Y. St. Bot.* 44: 134. 1891; *M. globisporum* Donk; *Leptoglossum*, Corner)

\*\*if it is permitted to consider the (slight) "membranal" pigment as a necropigment.

*Practical importance:* Not known (possibly a wood destroyer).

## SPECIES

*C. digitalis* (A. & S. ex Pers.) Fr. (*Aleurodiscus*, Donk).

### Reduced series: 65. PHAEODEPAS Reid

*Kew Bull.* 15: 273. 1961.

*Type species:* *P. dennisii* Reid.

**Characters:** Carpophores campanulate-cupuliform, pendulous or recurved-nutant with or without a lateral stipe, pigmented, the hymenial surface smooth or with a few veniform radial elevations, insititious or not; spores hyaline, smooth, thin-walled, or firm-walled, inamyloid, acyanophilic, ellipsoid or oblong, often with a rather long sterigmatal appendage; basidia normal, 4-spored, without basal clamp, sometimes with a slight constriction, not siderophilous; cystidia none; trama of the pileus monomitic, but sometimes strongly cyanophilic, filamentous hyphae found among the broader acyanophilous ones, all without clamp connections and inamyloid, not gelatinized, thin- to thick-walled and often constricted at the septa, irregular towards the subhymenium which consists of variously shaped, often short elements and is poorly differentiated from the hymenopodium, the firm- to thick-walled hyphae with sparse septa and wall up to 1  $\mu\text{m}$  thick, towards the sterile surface predominantly radially arranged and broader and more firm- to thickish-walled, either all repent and simple and smooth or with scattered small outgrowths, knobs or spinules on the epicuticular outermost elements, only on the stipe or pseudostipe surface (if present) often an intermittent Rameales-structure, and hyphae of the stipe parallel with each other and likewise inamyloid. Pigment intracellular or intraparietal, but never incrusting, sometimes absent in pileus but then present in the mature stipe. On dead leaves and culms or petioles, and on pteridophyte fronds, the hymenial surface directed downwards.

*Development of the carpophores:* Unknown.

*Area:* South America.

**Limits:** The genus is well delimited from the related genera of the Collybieae because of the absence of clamp connections and the habitat. The second species now known has an intermittent Rameales-structure on the stipe, and this permits the insertion of this genus in the Collybieae, Tricholomataceae.

*State of knowledge:* Two species are well known and published.

*Practical importance:* Unknown.

## SPECIES

*P. dennisii* Reid; *P. nutans* Sing. Two other South American species have been studied by me (unpublished).

### Reduced series: 66. CALYPTELLA Quél.

*Enchir.* F., p. 216. 1886.

*Type species:* *Cyphella capula* (Holmsk. ex Fr.) Fr. *sensu* Donk\*.

*Syn.:* *Metulocyphella* Agerer, *Zeitschr. f. Mykol.* 49: 155. 1983.

*Incrustatocalyptella* Agerer, l.c. p. 160.

*Characters:* Habit pezizoid-cyphelloid, carpophores small, often attached laterally to a pseudostipe, concave above, with smooth hymenial surface. Pigment none, or if present, often incrusting the walls of the trama and/or the cortical sterile layer of the outside of the cup which has typical *Rameales*-structure (irregular hyphae, often branching, with small obtuse branchlets, knots, diverticulations, or cauliflower and coral structures - not regularly diverticulate hyphae as in *Mycena* or dichophysoid bodies as in *Resupinatus* subg. *Asterotus*!); hyphae typically with clamp connections and not gelatinized, inamyloid. Spores hyaline, smooth, typically medium sized, short ellipsoid to oblong ellipsoid, inamyloid, thin-walled. On stems or leaves of herbaceous plants, also on woody remainders, mainly on dead vegetable trash.

*Development of the carpophores:* Gymnocarpous; stipitocarpous (?) see Watling (1985).

*Area:* Probably cosmopolitan.

*Limits:* Among the cyphelloid genera, this is unique because of its truly cyphelloid habit and *Rameales*-structure of the outside of the cup. See also under *Fistulina* (p. 843).

*State of knowledge:* This is a genus with numerous species; many have apparently been described, but relatively few are well known. Six species are enumerated below.

*Practical importance:* It is probable that there are some parasitic species among the Calyptellas; whether they damage the crops is unknown.

## SPECIES

Subgenus I. **Calyptella.** Carpophores rising gregariously from the substratum.

\*Spores 8-8.5 × 5-6 µm; pseudostipe up to as long as height of cup, pruinose, insititious; hyphae with clamp connections; on potato. This is represented by a collection by N. E. Nannenfa-Bremenkamp from Doorwerth, Netherlands (L.). This concept is clearly included in Quélet's and fits *C. campanula* (Nees ex Pers.) W.B. Cooke ss. W. B. Cooke. *C. capula* sensu Bourdot & Galzin has narrower spores. Singer (1951) tentatively proposed *Cyphella musicola* as type, a species closely related. Neither has a stipe and could not be stipitocarpous.

*Type species: C. capula* (Holmsk. ex Fr.) Quél.

*C. capula* (Holmsk. ex Fr.) Quél.; *C. musaecola* (Berk. & Curt.) Sing.; *C. epibrya* Sing. \*; *C. flava* Sing.; *C. pteridophytorum* Sing.; obviously also *C. cylindrospora* Reid and many other cyphelloid species \*\*.

Subgenus II. **Syncyphella** Sing. (1973). Carpophores rising mostly in bunches or rows from a common amorphous or clavate protocarpic body.

Type and only species: *C. bonaerensis* Sing. (also perhaps here *Glabrocyphella ailanthi* W.B. Cooke).

### Tribus Resupinateae Sing.

*Sydowia* 2: 30. 1948.

Type genus: *Resupinatus* Nees ex S.F. Gray.

**Characters:** Those of the family: hymenophore lamellate or none; basidia normal, i.e. not the *Lyophyllum* type; spores hyaline, punctate-rough or smooth, inamyloid, globose to short-ellipsoid, in some species also allantoid (curved) or ellipsoid-oblong with the inner side applanate, or ovoid; cheilocystidia usually present but not always conspicuous; metuloids (Pl. 18) often present on the sides of the lamellae; stipe rarely normally developed, often lateral and then the carpophores assuming a peculiar spatulate shape, or - most frequently - replaced by a pseudostipe which may be lateral (a mere prolongation of the rear side of the pileus, recognizable as a pseudostipe from below rather than from above), or else a discal pseudostipe; context soft and usually flexible when fresh, not becoming tough, consisting of inamyloid tissue which is usually at least partly gelatinized (Pl. 29), if not gelatinized at all, pigmented metuloids present; the hyphae of the gelatinous layers thin, wavy, thin-walled, with clamp connections. Most frequently on decaying wood, more rarely on other vegetable matter in process of decomposition, or on diseased living tissue of Cormophyta. Imperfect stages of many species of *Hohenbuehelia* belong to *Nematoctonus* Drechsler (Hyphomycetes) and are nematophagous. It is not clear, however, whether the type species of *Nematoctonus* belongs in the Resupinateae.

The Resupinateae are a group of closely related genera, inseparable one from another, and forming a very natural tribus. They are, on one hand, close to the Collybieae particularly such genera as *Marasmiellus* and *Campanella*, on the other the Panelleae, particularly *Panellus*. They may also be a connecting link with a

\* Possibly to the preceding genus because of the lack of clamp connections.

\*\* *Incrustatocalyptella* and *Metulocyphella* differ from the species enumerated here in crystalline encrustation of the elements of the Rameales structure or ramosc apices of the terminal cells of the epicutis hyphae; *Metulocyphella* besides in hymenial metuloids. I have not studied the species involved (*I. columbiana* and *pseudopanacis* (Agerer) Agerer; *M. lanceolata* and *rostrata*) which are well described by Agerer (l.c.) and may deserve one or two sections of their own.

family now generally considered aphyllophoraceous viz. the Fistulinaceae (see under *Fistulina*, p. 843).

As for the differences of *Marasmiellus* and *Campanella* from *Resupinatus*, see the latter genus.

#### KEY TO THE GENERA

- A. Metuloids or similar ± thick-walled cystidia present.
  - B. Carpophores centrally stipitate and without any gelatinization; metuloids distinctly pigmented. 68. *Agaricochaete*, p. 341
  - B. Carpophores rarely centrally stipitate, usually with a distinct gelatinous zone in the trama; metuloids (in KOH) hyaline or slightly pigmented (fuscidulous or pale melleous) 69. *Hohenbuehelia*, p. 341
- A. Metuloids absent, only thin-walled cheilocystidia present.
  - C. Hymenophore constantly lamellate. 67. *Resupinatus*, p. 339
  - C. Hymenophore absent. (see key p. 392)

#### 67. RESUPINATUS Nees ex S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 617. 1821.

*Type species:* *R. applicatus* (Batsch ex Fr.) S.F. Gray.

*Syn.:* *Phyllotus* Karst., *Bidr. Finl. Nat. Folk.* 32: 14 1879\*.

*Scytinotopsis* Sing., *Ann. Mycol.* 34: 335. 1936, *nom. nud.*

*Asterotus* Sing., *Mycologia* 35: 161. 1943.

**Characters:** Those of the tribus; carpophores pleurotoid, rarely omphalioid, and then stipitate (and blackish in all parts), otherwise with a lateral stipe or pseudostipe which is not differentiated from the pileus, or without stipe or with a pseudostipe attached to the sterile surface of the pileus; epicutis often consisting of a stratum of asterostromelloid hyphae (Pl. 37) or a *Rameales*-structure; spores globose, ellipsoid-ovate, allantoid, or oblong to cylindric, smooth, inamyloid, acyanophilic; basidia normal; cystidia none; cheilocystidia mostly present but often replaced by a band of asterostromelloid or *Rameales*-structure; hyphae in the monomitic trama generally gelatinized at least in a definite stratum of the pileus and/or the hymenophoral trama, which is regular, but hyphae often strongly interwoven, at least in part of the hymenophore; hymenophore always present, lamellate, lamellae concurrent or decurrent; veil none. Basal mycelium usually well developed. Base of basidia and hyphae clamped. Pigment present, frequently intraparietal and incrusting. On wood and grasses or other herbaceous plants, rarely on living plants; the hymenophore facing downwards.

\*The first authors who proposed a lectotype independently of the first-species rule, i.e. actually selected a type according to the Code, were Singer & Smith; *P. applicatus*.

*Development of the carpophores:* Gymnocarpous stipitocarpous. *Nematoctonus*-anamorphs not formed.

*Area:* Almost cosmopolitan.

*Limits:* This genus should be compared with other agarics having gelatinized trama. Among the pleurotoid ones, gelatinized trama is also found in *Marasmiellus* and *Campanella*. The *Marasmielli* with gelatinous trama are practically devoid of pigments or else have spores with bulges or triangular outline; they have an eccentric insititious or subinsititious stipe. *Campanella* can be distinguished by the different (or absent) pigments and favoloid-alveolar hymenophore. Among the stipitate forms there is only one species in *Resupinatus* which differs from all other agarics with gelatinized trama by the omphalioid habit combined with intraparietal and incrusting pigment which is dark, and present in all parts of the carpophore. It might only be mistaken for *Micromphale* which contains a single species with gray lamellae (*M. griseum*); this has pleurocystidia, adnexed lamellae, and fusoid basidioles.

*State of knowledge:* 11 species are now well known.

*Practical importance:* Practically none as far as present information is concerned.

## SPECIES

Subgenus **Omphalinoides** Sing. (1975). Stipe well developed, central or eccentric.

Type and only known species: *R. omphalinoides* Sing. in Sing. & Moser.

Subgenus **Asterotus** (Sing.) Sing. (1972). Stipe not differentiated, but a lateral extension of the pileus is definitely stipe-like; pileus lateral, sometimes with paler zones; epicutis asterostromelloid (Pl. 37); lamellae deeply decurrent on one side of the "stipe"; pileus about 14-45 mm in diameter. Thermophilous species, mostly in tropics and subtropics. Lignicolous.

Type species: *Panus dealbatus* Berk.

*R. dealbatus* (Berk.) Sing.; *R. bicolor* (Mont.) Sing. (*Panus sprucei* Berk.).

Subgenus **Resupinatus** (*Geopetalum* subgen. *Phyllotus* (Karst.) Kühner & Romagnesi). Carpophores pleurotoid, pendulous, without stipe, sessile or with a pseudostipe attached to the sterile surface; epicutis asterostromelloid, or a *Rameales*-structure, or scarcely differentiated; lamellae concurrent at a lateral or eccentric or central point of the fertile (lamellate) side, sometimes ascendant, mostly subhorizontal; pileus convex, cup-shaped, bell-shaped or companulate-cylindrical, 1-30 mm broad. Species of the tropical as well as the temperate zones. Lignicolous or graminicolous (on grasses and Bambuseae) or on herbaceous débris.

Type species: *R. applicatus*-(Batsch ex Fr.) S.F. Gray.

*R. applicatus* (Batsch ex Fr.) S.F. Gray (sensu Kauffman); *R. striatulus* (Fr.) Murr. sensu Coker; *R. trichotis* (Pers.) Sing. (*R. rhacodium* (Berk. & Curt.) Sing.); *R. sub-rhacodium* Sing.; *R. unguicularis* (Fr.) Sing.; *M. graminum* (Sing.) Sing.; *R. alboniger* (Pat.) Sing. (*R. argentinus* (Sing.) Sing.); *R. chilensis* Sing.

## 68. AGARICOCHAETE Eichelbaum

*Verhandl. Naturwiss. Ver. Hamburg* 3(14): 58. 1906.

*Type species:* *A. mirabilis* Eichelbaum.

*Characters:* Habit omphaloid to almost clitocyboid; trama non-gelatinized; metuloids present, conspicuous, inamyloid, pigmented; cheilocystidia differentiated, thin-walled, much like those of *Hohenbuehelia*; spores ellipsoid to cylindrical, thin-walled, inamyloid; basidia normal for the tribus; hyphae with clamp connections, inamyloid; hyphal system monomitic; hyphal walls thin; epicutis - a cutis of repent, parallel hyphae; hymenophoral trama subregular. On the ground.

*Development of the carpophores:* Unknown.

*Area:* Tropical Africa.

*Limits:* The genus was originally described on the base of two East African species but the data given by the original author were insufficient to separate this genus from similar ones. However Pegler (1977) was able to study a third, undoubtedly congeneric species from the same general area and thanks to him we can now insert it in the Resupinateae. The data in the paragraph on "Characters" are taken from his account (l.c., p. 98-100). As he states correctly, *Agaricochaete* differs from *Geopetalum* (Polyporaceae) in monomitic hyphal system, in inamyloid metuloids, heteromorphous lamella edge with cheilocystidia much like those of *Hohenbuehelia*.

*State of knowledge:* While the original two species are still insufficiently described, *A. keniensis* is now well known. The types are not where Eichelbaum deposited them.

*Practical importance:* Unknown.

## SPECIES

*A. keniensis* Pegler; apparently also *A. mirabilis* Eichelbaum and *A. hericium* Eichelbaum.

## 69. HOHENBUEHELIA Schulz. apud Schulzer, Kanitz & Knapp

*Verhandl. zool.-bot. Ges. Wien* 16: 45. 1866.

**Type species:** *H. petalooides* (Bull. ex Fr.) Schulz. apud Schulz., Kanitz & Knapp sensu Schulz.

**Syn.:** *Pleurotus* sect. *Acanthocystis* Fayod, Ann. Sc. Nat. Bot. VII: 338. 1889.

*Pleurotopsis* (Henn.) Earle, Bull. N.Y. Bot. Gard. 5: 412. 1900\*.

*Phyllospadix* Lloyd, Myc. Writ. 6: 1007. 1920\*\*.

*Acanthocystis* (Fayod) Kühner, Contrib. Hymen. (Thèse) p. 111. 1926.

*Conchomyces* Van Overeem, Bull. Jard. Bot. Buitenzorg 9: 19. 1927.

*Urceolus* Velen., Nov. Myc. p. 38. 1939.

**Characters:** Those of the tribus; metuloids (Pl. 19) present and usually distinctly thick-walled (with mostly several wall layers which are hyaline or pigmented) and with a covering of coarse to finely granular crystals apparently of calcium oxalate, the apex obtuse or more often acute, usually on both edges and sides of the lamellae; otherwise much like *Resupinatus*, with all the types of carpophores occurring there, and usually but not always partially gelatinized trama (most frequently a layer of gelatinized tissue forming the upper layer of a bistratous pileus-trama, and the hyphae there separated by a mucous mass, thin-walled and thin-filamentous, clamped, hyaline, rarely fuscidulous, horizontal or obliquely ascendant, more rarely interwoven and here endocystidia at times occurring, Pl. 30); carpophores pleurotoid, often with a spatuloid appearance and then the pileus recurved to a horizontal position, but the stipe in most species not sharply differentiated from the pileus when seen from above: "petaloid"); spores either (mostly) smooth, or asperulate-punctate, inamyloid, acyanophilic. Pigment present or absent; cheilocystidia mostly differentiated and thin-walled; clamp connections present; hyphae inamyloid; trama monomitic (but not all of the same kind). On the ground, on wood, and on culms and stipes of Monocotyledones, also on living and dead *Pycnophyllum*, *Azorella*, and *Stipa* in the alpine zone of the Andes. - Imperfect forms are *Nematoctonus* species capturing nematodes. (Thorn, pers. comm., see also Thorn & Barron (1984) and Barron & Dierkes (1977).

**Development of the carpophores:** Gymnocarpous, stipitocarpous. *Nematoctonus*-anamorphs generally formed.

**Area:** Almost cosmopolitan.

**Limits:** The characteristic metuloids have induced some authors to assume that other white-spored pleurotoid species belong in the affinity of *Hohenbuehelia*, but this is not always the case. *Geopetalum* differs in the absence of a gelatinous layer, pseudoamyloid metuloids, and dimitic trama. *Campanella* differs in the configuration of the hymenophore and lack of a basal mycelium.

**State of knowledge:** We know now 30 species of *Hohenbuehelia*.

**Practical importance:** Some *Hohenbuehelia*s are occasionally parasitic on forest and fruit trees. Some are reported to be edible, but their economic importance is small; at least one species is a possible source of an antibiotic substance, pleurotin (*Proc. Nat. Acad. Sc.* 33: 176. 1947).

\*On the type species of this genus see Singer in Donk, *Nov. Hedw.* 5: 237. 1962.

\*\*The type species, *P. africana*, has thick-walled cystidia. Horak interprets these as different from metuloids, and thinks that this species belongs to *Resupinatus*.

## SPECIES

Subgenus **Hohenbuehelia**. Spores smooth; gelatinous layer present, rarely absent or not sharply differentiated from the lower layer.

Type species: *H. petalooides* (Bull. ex Fr.) Schulz. apud Schulzer, Kanitz & Knapp (sensu Schulzer).

Stirps *Petaloides* (habit petaloid).

*H. petalooides* (Bull. ex Fr.) Schulz. apud Schulz., Kanitz & Knapp (sensu Huijsman) (*H. auriscalpium* (Maire) Sing.; *Acanthocystis*, Konr. & Maubl.); *H. geogenia* (D.C. ex Fr.) Sing. (*H. petalooides* sensu Schulz. according to Huijsman); *H. semiinfundibuliformis* (Karst.) Sing.; *H. alachuana* (Murr.) Sing. (if not too close to *H. geogenia*); *H. rickenii* (Kühn.) Kühn. ex Orton (*Pleurotus geogenius* sensu Bresadola according to Huijsman); *H. pycnophylli* Sing.; *H. angustata* (Berk.) Sing. (*Acanthocystis stratos* (Atk.) Sing.); *H. pergelatinosa* Sing.; *H. abietina* Sing. & Kuthan; *H. izonetae* Sing. ined.; obviously also *H. spatulina* Huijsman.

Species with poorly developed gelatinosity: *H. spegazzinii* Sing.; *H. roigii* Sing.

Species with often central stipe: *H. longipes* (Boud.) Moser in Gams (*Omphalia aulacomnii* J. Schäffer); obviously also *H. culmicola* Bon.

Species with indistinct (less projecting, less thick-walled) metuloid cystidia: *H. cyphelliformis* (Berk.) Miller; *H. silvanus* (Sacc.) (*Resupinatus*, Sing.), probably conspecific with the preceding species; *H. unguicularis* ("Fr.") sensu Lange, Kühner & Romagnesi (non Fr.) Miller.

Stirps *Atrocaerulea* (habit not petaloid).

*H. atrocaerulea* (Fr.) Sing.; *H. algida* (Fr.) Sing. (*Agaricus albidus* Fr., Syst. 1: 190. 1821; *Hohenbuehelia fluxilis* (Fr.) Orton); *H. portegna* (Speg.) Sing.; *H. phalligera* (Mont.) Sing.; *H. bullulifera* Sing. in Sing. & Digilio; *H. calongei* Sing.; *H. paraguayensis* (Speg.) Sing.; *H. cubensis* (Murr.) Sing.; *H. approximans* (Peck) Sing.; *H. nigra* (Schwein.) Sing. with var. *microspora* Sing.; *H. mastrucata* (Fr.) Sing.; *H. myxotricha* (Lév.) Sing.; *H. reniformis* (Fr.) Sing. (sensu Pilát; *Pleurotus applicatus* (Batsch ex Fr.) Kummer sensu Quél., Karst. non al.; *Pleurotus mustaliensis* Karst.); obviously also *H. repanda* Huijsman, *H. sciadia* (Kalchbr. & McOw.) Sing., and *H. chevalieri* (Pat.) Pegler.

Note: Huijsman erects a new subgenus for *H. mastrucata* and similar species where the gelatinous layer is at least as deep as the non-gelatinized lower layer of the pileus trama. However, on the basis of Huijsman's diagnosis, some cases remain doubtful because the diameter of the gelatinous layer - for example in *H. atrocaerulea* - is as broad as the subjacent trama in the marginal zone of the pileus whereas in the central zone the non-gelatinous layer is distinctly broader. In species closely related to those where the gelatinous layer is at least equal to the non-gelatinous, and where we cannot admit a separation into a different subgenus (or section) - for example in *H. phalligera* - the gelatinous layer is 300-450 µm thick (in KOH) and the subjacent

non-gelatinous layer 550-600  $\mu\text{m}$ . To be acceptable, the subgenus *Omphalaria* Huijsman if at all necessary, would have to be redefined. This can only be done on the basis of a world monograph of the genus as a whole.

Subgenus **Reidia** Sing. (1969). Spores asperulate-punctate, finely spinulose (but acyanophilic). Temperate zone of the Southern Hemisphere, north to Java; also in East Africa.

Type species: *Agaricus bursaeformis* Berk.

*H. bursaeformis* (Berk.) Reid (*Crepidotus interceptus* (Berk.) Sacc.); *H. dimorphocystis* Sing.

Note: Horak was kind enough to show me his copy of the original drawings and notes on *Conchomyces* (which he identified with *Hohenbuehelia* sg. *Reidia*). This material does not fully disprove the interpretation of *Conchomyces* as a *Crepidotus*. Only in Horak's further studies (1981) in which he compared material which is topotypical (from Java, Indonesia) for *Conchomyces verrucisporus* Van Overeem with the Australian types, was the identity satisfactorily established. Yet my own descriptive data from the type and from South American material do not bear out any conclusion that *Conchomyces* is independent from the genus *Hohenbuehelia*. Neither have all Hohenbuehelias "allantoid-cylindric" spores nor are the cystidial characters sufficiently different and the spore ornamentation alone does not justify a separate genus even less a genus without obvious relationships to any described taxa among the Agaricales as claimed by Horak. If *H. bursaeformis* actually does occur in East Africa (cf. Pegler (1977, p. 104), its distribution is much wider than suggested by Horak. Furthermore Horak's characterization of subgenus *Reidia* as "heterogenous" is difficult to understand since he considers (l.c. p. 110) the only two species enumerated in this subgenus by me as identical with each other.

#### Reduced series: 70. STIGMATOLEMMA Kalchbr.

*Grevillea* 10: 104. 1882.

Type species: *S. incanum* Kalchbr.

Syn.: *Rhodocyphella* W.B. Cooke, *Beih. Sydowia* 4: 105. 1961.

Characters: Habit pezizoid or poroid-concrescent ("Solenia"), and then often imbedded in a white stroma or extensive white basal mycelium, small with smooth mostly gray hymenial surface. Spores subglobose to ellipsoid, or short-cylindric, sub-allantoid, sometimes weakly angular smooth, inamyloid; basidia rather short, (2)-4-spored, without siderophilous granulation; cystidia none; sterile surface not clearly individualized from stroma which consists of very thin hyaline hyphae which are often incrusted by a hyaline granulation and smooth, or with lacerate or subcapitate apex; trama of pileus often fuscous with an often partially intraparietal pigment but mostly without pigment incrustations, dense and of subparallel hyphae in a layer near the hymenium, hyaline and gelatinized in an external layer,

inamyloid, with numerous clamp connections. On dead wood and stems.

*Development of the carpophores:* Unknown

*Area:* Probably almost cosmopolitan.

*Limits:* Among the Agaricales, this can only be compared with *Resupinatus* from which it differs in the complete absence of lamellae. We do not share the opinion of W.B. Cooke (*Mycologia* 49: 680-693) who considers *Stigmatolemma* congeneric with *Porotheleum* [with *P. fimbriatum* (Pers. ex Fr.) Fr. as type species] nor do we consider the family Porotheleaceae Murr. a natural unit as delimited by this author. Likewise, we do not agree with the synonymization of *S. incanum* with *S. poriaeforme* and the general description for these species as given, *l.c. p. 689*, does not agree with our own observations in several important details.

*State of knowledge:* Species belonging here have often been overlooked or misdetermined in the past. Personally, I have thoroughly studied only two species but at least six more seem to belong in this genus.

*Practical importance:* Unknown.

## SPECIES

*S. incanum* Kalchbrenner; *S. poriaeforme* (Pers. ex Mérat) W.B. Cooke; probably also *S. taxi* (Lév.) Donk.; *S. urceolatum* (Wallr. ex Fr.) Donk.; *S. conspersum* (Pers.) Donk., *S. farinaceum* (Kalchbr. & Cooke) Reid (as *S. farinacea*), *Lachnella myceliosa* Henn., and *Solenia huia* Cunningham.

## Reduced series: 71. STROMATOCYPHELLA W.B. Cooke

*Sydotia*, Beihefte 4: 104. 1961.

*Type species:* *Cyprella conglobata* Burt.

*Characters:* Carpophores densely conglobated, even laterally fused, small cups, often merging into a *Poria*-like fructification, arising from a common protocarpic resupinate layer; spores white in print, hyaline, inamyloid, cylindric to oblong, often slightly allantoid, smooth; basidia of variable length, 4-spored; hyphae gelatinized, with clamp connections, inamyloid, trama monomitic; cystidia none on the smooth hymenial surface; covering layer of the sterile surface with intraparietal pigment (also somewhat incrusting), forming a *Rameales*-structure with often individualized hair-like terminal members which are branched or otherwise diverticulate (branches and diverticula obtuse or acute) and tending to be thick-walled. On wood, according to Reid often or always associated with the stromata of Pyrenomycetes.

*Development of the carpophores:* Unknown.

*Area:* North America.

*Limits:* As given in the key (p. 392).

*State of knowledge:* Only one species can be recognized as belonging to this genus. Reid (1963) has shown that the other two species described under this generic name by W.B. Cooke are not congeneric.

*Practical importance:* Unknown.

## SPECIES

*S. conglobata* (Burt) W.B. Cooke.

Reduced series: 72. **APHYLLLOTUS** Sing.

*Sydotia* Beiheft 7: 29. 1973.

*Type species:* *A. campanelliformis* Sing.

*Characters:* Carpophores single, not aggregated on a stroma-like base, cup-shaped, later ear-shaped, hyphae above the hymenium which covers a smooth hymenial surface directed towards the ground, with incrusting dark pigment, gelatinized in the larger part of the pileus-trama; cystidia none; stipe none, but an eccentric or subcentral pseudostipe may be present; sterile surface covered with an asterostro-melloid to *Rameales*-structure; spores hyaline, smooth, but with an eccentric bulge (as often seen in *Campanella*) often well developed, medium sized, inamyloid; all hyphae inamyloid, with clamp connections. Lignicolous.

*Development of the carpophores:* Unknown.

*Area:* Neotropical (Colombia).

*Limitis:* As given in the key (p. 392).

*State of knowledge:* Only one species is known.

## SPECIES

*A. campanelliformis* Sing.

Tribus *Panelleae* Sing. ex Sing.

*Agaricales in modern taxonomy* 3rd ed., p. 337. 1975.

*Type genus:* *Panellus* Karst.

*Characters:* Those of the family; habit pleurotoid; consistency more or less tough

and reviving or gelatinous, mostly with a gelatinous layer in the trama of the pileus, more rarely without such a layer and then hymenophoral trama gelatinous or not; hyphal system monomitic; hyphae with clamp connections, inamyloid or weakly pseudoamyloid; spores amyloid, smooth, acyanophilic; pigments present or absent; epicutis of variable structure often with acantho-physoid hyphae or dermatocystidia, or an asterostromelloid or *Rameales*-structure present; hymenophore always present, either tubular to favoloid or, more frequently, lamellate; stipe present or more frequently absent or else merely an extension of the pileus not differentiated from above; veil present or absent. Carpophores often luminescent; on grasses and woody humus, débris, or (mostly) lignicolous.

#### KEY TO THE GENERA

- A. Veil present; spores weakly amyloid. 73. *Tectella*, p. 347
- A. Veil absent; development of the carpophores typically gymnocarpous and stipitocarpous.
  - B. Hymenophore lamellate, not anastomosing. 75. *Panellus*, p. 349
  - B. Hymenophore tubular to favoloid or at least lamellae strongly anastomosing with anastomoses as broad as the lamellae, typically reddening on drying 74. *Dictyopanus*, p. 348

#### 73. TECTELLA Earle

*Bull. N. Y. Bot. Gard.* 5: 433. 1909.

*Type species:* *Panus operculatus* Berk. & Curt. (= *Tectella patellaris* (Fr.) Murr.).

*Characters:* Pileus non-stipitate, attached laterally or at some point of the sterile surface; veil present in the form of a pellicular veil that covers the lamellae in the young specimens; spores up to 5.5 µm long, small, almost inamyloid but in accumulations amyloid, acyanophilous, smooth. Basidia normal, 4-spored; basidioles not fusoid; cystidia none; but cheilocystidia differentiated and typically dimorphic, entire, obtuse, often thick-walled; trama of the pileus in its upper layer strongly gelatinized with thin-filamentous hyphae, in its lower layer non-gelatinous with thick-walled even solid hyphae which are interwoven and with clamp connections, sclerified generative hyphae, inamyloid, pigment present but not incrusting; hymenophore lamellate, lamellae not anastomosing, concurrent; hymenophoral trama subregular, of interwoven hyphae with an axillar trend, most ± thick-walled; epicutis not a *Rameales*-or astromelloid structure, non-gelatinous, brownish. Carpophores pendulous from a pseudostipe or directly attached to the substratum (wood), veil of strands of parallel hyaline hyphae, these inamyloid, thin-walled, thin-filamentous.

*Development of the carpophores:* Profoundly hemiangiocarpous: Bivelangiocarpous and pileocarpous or hymenocarpous, see Reijnders (*Bull. Soc. Myc. Fr.* 99: 110-126. 1983).

*Area:* Temperate Europe, Asia and North America.

**Limits:** This genus differs from all other astipitate veiled agarics by the amyloid spores and monomitic trama.

**State of knowledge:** Only one species is well known.

**Practical importance:** Wood destroyers; however, their comparative rarity prevents them from being seriously damaging to the timber industry in any particular region.

## SPECIES

*T. patellaris* (Fr.) Murr. (*Panus operculatus* Berk. & Curt.).

### 74. DICTYOPANUS Pat.

*Essai*, p. 137. 1900.

**Type species:** *Polyporus rhipidium* Berk. (= *Dictyopanus pusillus* var.).

**Characters:** Habit of the carpophores pleurotoid (polyporoid); epicutis of the pileus and the edges of the pores with strongly diverticulate hyphae, sometimes showing a distinctly dichophysoid structure; hymenophore favoloid or poroid; trama of the pore walls gelatinous or non-gelatinous, and then irregularly interwoven; basidia small to medium-sized, 4-spored; cystidia and/or cheilocystidia differentiated or replaced by dichophysoid structures; basidioles often fusoid; spores white in print, hyaline under the microscope, amyloid, smooth, small to medium (up to 7.8 µm), ellipsoid, oblong ellipsoid, or ellipsoid-cylindric; stipe lateral but often seemingly eccentric, comparatively short, often differentiated only below (and then hardly recognizable from above), or well individualized; trama mild, peppery, or astringent, tough; on wood and on grasses.

**Development of the carpophores:** Unknown but probably as in *Panellus* i.z. gymnocarpous.

**Area:** Predominantly tropical but also rarely occurring in temperate North and South America.

**Limits:** This genus is reminiscent of certain species of *Favolaschia*. It differs in hymenophore configuration, basidioles, pigment, and gelatinization. *Dictyopanus copelandii* resembles *Favolaschia* very closely but the author believes that - aside from phylogenetic speculation - there is no reason to assume that an immediate close affinity exists between *Dictyopanus* and *Favolaschia*; see also under this latter genus, p. 111.

**State of knowledge:** This genus has been treated in a paper on the *Laschia*-complex by R. Singer (*Lloydia* 8: 222. 1945), and all necessary data are now available on both species and varieties originally described by the present author. However, several apparently undescribed additional forms have come to my attention and others have been described recently so that a monographic treatment of *Dictyopanus* would be desirable.

*Practical importance:* Sometimes active wood-destroyers.

## SPECIES

*D. copelandii* Pat.; *D. pusillus* (Lév.) Sing. (*Gloeoporus*, Lév.; *Polyporus*, Persoon ex Lloyd; *Polyporus subpulverulentus* Berk. & Curt.; *Dictyopanus*, Pat.; *Laschia guaranitica* Speg.; *Gloeoporus*, Speg.) and its var. *rhipidium* (Berk.) Sing. (*Polyporus rhipidium* Berk.; *Favolus*, Sacc.; *Gloeoporus*, Speg.; *Dictyopanus*, Pat.), and var. *pseudorhipidium* Sing. (var. *sublamellatus* Corner); obviously also *D. luminescens* Corner.

## 75. PANELLUS Karst.

Hattsv., *Bidr. Finl. Nat. Folk* 32: xiv. 1879.

*Type species:* *P. stypticus* (Bull. ex Fr.) Karst.

*Syn.:* *Scytinotus* Karst., l.c., p. xiv [type: *S. ringens* (Fr.) Karst.]

*Urospora* Fayod, *Prodr. Ann. Sc. Nat.* VII. 9: 338. 1889, *sensu* Fayod, non Earle; *non Urospora* Areschoug (1866) (Chlorophyceae)

*Sarcomyxa* Karst., *Soc. Fl. Fauna Fenn.* 18: 62. 1891.

*Urosporellina* Horak, *Beitr. Krypt.-fl. Schweiz* 13: 609. 1968.

*Characters:* Pileus rarely centrally (and then short-) stipitate, more frequently eccentrically or laterally stipitate or subsessile; epicutis consisting of filamentous hyphae which are more or less branched (Pl. 52, middle-right) and sometimes almost at right angles, in other cases merely nodulose at places, or simple and undivided, sometimes spirally twisted; spore print white or whitish; spores hyaline, cylindric, or ellipsoid to oblong, sometimes, allantoid, rarely short-ellipsoid, smooth, amyloid, acyanophilic; basidia normal, generally 4-spored, basidioles fusoid to narrowly clavate; cheilocystidia scattered to numerous, inconspicuous to conspicuous, rarely absent; cystidia or pseudocystidia present or absent, sometimes metuloid; dermatocystidia sometimes present; veil none; carpophores often luminescent, sometimes rising from an irregularly branched deep colored stroma-like base, more frequently directly from the substratum (wood, culms of Bambuseae, fern rachis etc.); trama of the pileus monomitic, often but not always with a gelatinous upper zone, hyphae inamyloid or very weakly pseudoamyloid, with clamp connections, filamentous or in part swollen-inflated as in *Hemimycena*, thin-to thick-walled; taste mild or stiptic, often distinctly reviving when dried and remoistened.

*Development of the carpophores:* Gymnocarpous and stipitocarpous in *P. mirabilis*, *mitis* (Singer) and *serotinus* (Reijnders).

*Area:* Almost cosmopolitan, but not outside the wooded areas.

*Limits:* *Panellus* can be easily distinguished from the other genera of the Panelleae by the characters indicated in the key. It differs from the Resupinateae and the

pleurotoid Collybieae and *Hemimycena* in the amyloid spores. Miller (1970) excluded *P. mirabilis* from *Panellus* (Pl. 57, right center) and transferred it to *Mycena*. However, it is different from *Mycena* since the trama is not of the *Mycena* type: its elements are, though often broad but not multiseptate-inflated, not parallel, not distinctly pseudoamyloid, but rather of the structure called sarcodimitic by Corner; the stipe is strictly eccentric in mature carpophores (which never occurs in *Mycena*), and the cystidia are pseudocystidia with an excretive function similar to the oleocystidia. This amorphous apical incrustation occurs frequently in *Panellus*, very rarely if at all in *Mycena*. Horak (1968) separates *P. mitis* generically from *P. stypticus* and the rest of *Panellus* on the strength of inamyloid spores which he also attributes to *Sarcomyxa*. However, the spores of both *Sarcomyxa* and *Urosporellina* (i.e. *Panellus mitis* and *P. serotinus*) are undoubtedly amyloid as has been stated earlier by Kühner, Kühner & Romagnesi, Kühner & Maire and myself.

*State of knowledge:* All 16 species are well known.

*Practical importance:* *P. stypticus*, and possibly other species, often is a wound-parasite which may, in combination with other pathogenic organisms, contribute to the death of valuable trees.

## SPECIES

Subgenus **Panellus**. Cystidia absent on the sides of the lamellae.

*Type species:* *P. stypticus* (Bull. ex Fr.) Karst.

*P. stypticus* (Bull. ex Fr.) Karst. [Panus, Fr.; Pleurotus, Pilat; Panus farinaceus (Schum. ex Fr.) Sacc.; *P. saccharinus* Berk.] with a luminescent and a non-luminescent race; *P. mitis* (Pers. ex Fr.) Sing.; *P. rupicola* (Mass.) Sing.; *P. belangeri* (Mont. ex Fr.) Sing. (*Trogia*, Mont. ex Fr.; Pleurotus, Dennis); *P. luteolus* (Speg.) Sing. (*Cantharellus*, Speg.); *P. longinquus* (Berk. in Hooker) Sing. (*Agaricus minusculus* Speg.; possibly also = *Panellus roseolus* Stevenson); *P. violaceofulvus* (Batsch ex Fr.) Sing.; *P. ringens* (Fr.) Romagnesi (*Lentinus michailowskoensis* Henn.; *Panus salicinus* Peck); apparently also *P. melleo-ochraceus* Malençon in Mal. & Bert. and *P. aureofactus* Horak.

Subgenus **Serotinia** (Pilat) Sing. Cystidia present on the sides of the lamellae, mostly thick-walled, but wall often remaining thin for a long period, mostly with some amorphous exudations deposited at the apex or all over, these resinous ("oleocystidia"), more rarely thin-walled and then with attenuate-subobtuse to acute apex.

*Type species:* *P. serotinus* (Pers. in Hofmann ex Fr.) Kühner.

1. Species with rather thin-walled, acute or attenuated, rarely clavate, scarcely incrusted cystidia. (This group might eventually better be placed in a separate section or subgenus). On Pteridophyta and Bambuseae, tropical and subantarctic.

*P. pteridophytorum* Sing.; *P. nubigenus* Sing. with ssp. *australis* Sing.; *P. stenocystis* Sing.

2. Species with mostly thick-walled, apically broadly rounded cystidia which are covered, entirely or at the apex, by a resinous exudation. Temperate and subtropical to tropical species, mostly lignicolous.

*P. serotinus* (Pers. in Hofmann ex Fr.) Kühner; *P. cystidiatus* Sing. in Sing. & Digilio; *P. luteus* (Dennis) Sing.; *P. mirabilis* Sing; *P. dumontii* Sing.; apparently also *Pleurotus cinereoalbus* Pat.

### Tribus *Marasmieae* Fayod ex Schröter

*Prodrome*, Ann. Sci. Nat. Bot. VII. 9: 340. 1889 (Marasmiés), em. Schröter in Cohn, *Crypt. Schles. Pilz.*, p. 553. 1889 ("Marasmieī"); Henn. in Engl. & Prantl, *Nat. Pfl.-Fam.* 1: 222. 1898; Ulbrich in Lindau, *Höh. Pilze*, p. 215. 1928; (*Marasmieī*) Fr., *Gen. Hym.*, p. 9. 1836, pro gen. typ. aliis exclusis).

Type genus: *Marasmius* Fr.

**Characters:** Basidia not siderophilous, and generally not longer than five times the length of the spores; habit collybioid to mycenoid or omphalioid, often reviving when dried and remoistened, also pleurotoid, i.e. with eccentric, often short and curved, or completely reduced or functionless stipe, or cyphelloid i.e. *Otidea-* or *Peziza*-like and small with or without pseudostipe, with a lateral stipe or without stipe, rarely clavarioid, with a hollow, stipitate head covered by hymenium; hymenophore lamellate, more rarely lamellae so strongly anastomosing that they are almost poroid or meruliod, or else entirely wanting (with smooth hymenial surface); epicutis with broom cells or with smooth (without setulae) cells, in the first case often, in the latter case always forming a hymeniform, subhymeniform layer, or a trichodermial palisade of broad, parallel or subparallel pigmented (intraparietal pigment), erect elements, or with very long incrusted or pseudoamyloid hairs, more rarely the hairs inamyloid and with pseudoamyloid, flagella-like appendages, rarely with repent, nodulose-diverticulate hyphae (but then trama pseudoamyloid or spores not smooth or with a very prominent hilar appendage and subglobose), gelatinous or not, often with dermatocystidia; hymenophoral trama regular (not bilateral except in the primordia) when present. Trama of the pileus monomitic (but sometimes hyphae of two kinds, yet always without true skeletal hyphae and ligative hyphae, but sometimes with deep-rooting setose cystidia); cheilocystidia and often also pleurocystidia present, these thin- or thick-walled, sometimes pseudocystidioid or broom-cells, or metuloid; base of stipe with basal mycelium or insititious; sometimes rising from dark rhizomorphs; hyphae of the trama of the pileus or at least the stipe pseudoamyloid or inamyloid (and then epicutis with broom cells and mostly hymeniform), with or without clamp connections. Spores inamyloid, more rarely pseudoamyloid, hyaline, smooth, or finely rough, verrucose or spinose, small to enormously long or voluminous, acyanophilic or cyanophilic; never mycenoid to omphalioid and all white and with basal mycelium; never mycenoid or omphalioid with the stipe separated from the pileus-trama by a separation layer; never soft-

mycenoid to omphaloid with basal mycelium and diverticulate or smooth appressed hyphae or with a powdery layer of acanthophysoid cells; pseudorrhiza or radicant immersed portions of the stipe often present; telopods often formed; lichenization and ectomycorrhiza never observed.

#### KEY TO THE GENERA

- A. Pseudoamyloid or incrusted long hairs, or hairs with apical flagella-like pseudoamyloid appendages present on the surface of the pileus, sometimes also the stipe, and the surfaces therefore hairy; spores sometimes inamyloid, other times pseudoamyloid, usually cyanophilic; habit collybioid to pleurotoid, or cyphelloid; trama of the pileus and the hymenophoral trama inamyloid.
- B. Hymenophoral trama present, lamellate.
- C. Hairs merely with flagella-like pseudoamyloid appendages at their apex.
    - 80. *Amyloflagellula*, p. 385
  - C. Hairs pseudoamyloid in the lower portion, thick-walled, usually very long.
    - D. Stipe present and functional, insititious or more rarely with basal mycelium.
      - 78. *Crinipellis*, p. 380
    - D. Stipe absent and often replaced by a pseudostipe, or minute and functionless.
      - 79. *Chaetocalathus*, p. 384
  - B. Hymenophoral trama absent. (See key II, p. 392)
  - A. Pseudoamyloid elements on the surface of the pileus not in form of hairs, nor of flagella-like apical appendages on the latter, nor in form of long incrusted hairs; if there are pseudoamyloid elements on the pileus surface, these are in form of broom cells or cystidiform; spores inamyloid, acyanophilic or cyanophilic; habit as above or different; trama of the pileus pseudoamyloid or inamyloid.
  - E. Hymenophore absent, or reduced to very low obtuse veins. (See key II, p. 392)
  - E. Hymenophore always present in form of narrow, almost vein-like lamellae, or in form of broad lamellae which may be intervenose.
  - F. Epicuticular hyphae smooth and entire, forming a hymeniform or subhymeniform layer; stipe more or less radicant, more rarely not so, neither eccentric nor setiform and dark, nor insititious; habit collybioid, rarely almost tricholomatoid; pileus sometimes viscid; spores medium to large and relatively broad (always broader than 7.5  $\mu\text{m}$ ) if hyphae have clamp connections; trama of the pileus and stipe inamyloid; pleurocystidia usually large and conspicuous.
  - G. Spores smooth or spinose and medium sized to voluminous, weakly cyanophilic in an outer layer, usually rather broad, even globose; epicutis hymeniform; pileus often relatively fleshy, not reviving clamp connections present.
    - 76. *Oudemansiella*, p. 354
  - G. Spores smooth, small to medium sized, ellipsoid to oblong, acyanophilic; clamp connections absent; radicant on immersed conifer cones and various inflorescentia. Pileus never glutinous. Usually on cones of conifers or *Magnolia* (if on Monocotyledones see "K" below)
    - 79. *Strobilurus*, p. 359
  - F. Epicutis as indicated above; or different; stipe as indicated above or different; spores as indicated above, or different; trama of the pileus pseudoamyloid or inamyloid; pleurocystidia present or absent; clamp connections present or absent; never combining all the characters indicated above. If the trama is inamyloid and the epicutis hymeniform and clamp connections present, the stipe is never long-radicant and the pileus never hairy or glutinous.
  - H. Spores either rough-asperulate or verruculose or spinulose, or punctate because of heterogenous spore wall (ornamentation XI), or subglobose and smooth, and with a relatively voluminous hilar appendage acyanophilic; trama inamyloid; habit mycenoid, rarely almost collybioid, not reviving, not with dark dark seta-like stipe nor with black rhizomorphs; epicutis not hymeniform but often with numerous erect, conspicuous dermatocystidia, elements of the epicutis often diverticulate; stipe not insititious.
    - 77. *Mycenella*, p. 356
  - H. Spores smooth and hilar appendage not particularly voluminous if the spores are subglobose; trama pseudoamyloid or inamyloid; habit collybioid or mycenoid, or else pleurotoid, reviving or not, stipe insititious or not, dark and seta-like or not, black

rhizomorphs present or absent; epicutis as above or different. Never combining all the characters indicated above.

- I. Epicutis consisting of a trichodermial palisade of parallel or subparallel rather broad, mostly elongated hyphal cells with intraparietal pigment (usually deep cinnamon) or all hyphal cells so short as to produce an epithelium or the epicutis consists of a deep trichodermium which is ± fractured to form soft floccos; no broom cells present; habit collybioid or almost omphaliod; stipe not radicant; hyphae inamyloid.
  - J. Epicutis a trichodermal palisade with parallel or subparallel rather broad but mostly elongated cells with intraparietal pigment (KOH) which is persistent, cinnamon; no gelatinization anywhere in the trama or covering layers; cystidia broad; clamp connections present; spores longer than 5  $\mu\text{m}$  and up to 7.5  $\mu\text{m}$ , white in print. Neotropical  
78. *Physocystidium*, p. 358
  - J. Epicutis, or spores or cystidia different; clamp connections present or absent (see trib. *Pseudohiatuleae*, p. 433)
- I. Epicutis different, either hymeniform, or with broom cells, or both.
    - K. Small to minute carpophores with hymeniform epicutis containing conspicuous, often capitate or subcapitate dermatocystidia or long hairs (or both), or the epicutis elements exuding brown resinous matter and not in form of broom cells; lamellae often rather few or reduced; stipe often branched or eccentric; pileus not over 6 mm broad, rarely reaching 10(11) mm diam. and then stipe eccentric; trama of the pileus inamyloid (see key II, p. 392).
    - K. Minute to large carpophores with hymeniform or not hymeniform epicutis; if the epicutis is hymeniform, it consists of (or contains many) broom cells or the pileus is larger than 10 mm when mature, or the trama of the pileus is pseudoamyloid, or there are neither conspicuous, long hairs nor capitate dermatocystidia present.  
80. *Marasmius*, p. 360

### Subtribus *Oudemansiellinae* Sing.

*Sydowia* 5: 58. 1961.

Type genus: *Oudemansiella* Speg.

**Characters:** Those of the tribus. Spores, hyphae, and epicutis inamyloid. Epicutis consisting of a hymeniform layer or a trichodermial palisade of rather short elements, or of scattered but numerous conspicuous dermatocystidia (and the spore print pink, or pileus glutinous), often with dermatocystidia, pilose elements (sometimes even macroscopically visible) or metuloids (but not gloeocystidia) interspersed in the hymeniform epicutis or palisade; habit generally collybioid or mycenoid; spores often with a relatively very voluminous hilar appendage or ornamented and in this latter case, the dermatocystidia or hymeniform layer of the epicutis of the pileus sometimes missing. Base of stipe sometimes radicate (with a pseudorrhiza) or with basal tomentum or mycelial fibrils, rarely insititious but may be deeply inserted and then generally with a double veil, otherwise never with a veil; clamp connections present or absent.

## 76. OUDEMANSIELLA Speg.

*Ann. Soc. Cient. Arg.* 12: 24. 1881.

Type species: *O. platensis* (Speg.) Speg.

Syn.: *Oudemansia* Speg. *An. Soc. Cient. Arg.* 10: 280. 1880 non Mig. 1854 (Sterculiaceae).

*Mucidula* Pat., *Hymen. Eur.*, p. 95. 1887.

*Phaeolimacium* Henn. in Warburg, *Monsunia* 1: 14. 1900.

*Gymnopus* (Pers.) Roussel ex Earle, *Bull. N.Y. Bot. Gard.* 5: 428. 1909 (see footnote under *Mycena*, p. 401).

*Xerula* R. Maire, *Publ. Junta Cienc. Nat. Barcelona*, p. 66. 1933.

*Dactylosporina* (Clémenton) Dörfelt, *Fedde's Rep.* 96: 236. 1985.

(?)*Coprinopsis* Beeli, *Bull. Soc. R. Bot. Belg.* 61: 98. 1928, non Karst. (1881).

**Characters:** Habit of the carpophores collybioid, rarely collybioid-mycenoid; carpophores often large, often pigmentless or almost so, or with a fuscous gray, black, brown to olive, rarely blue pigment; pileus often rather fleshy, dry or viscid to glutinous; cuticle of the pileus bearing a hymenium of broad elements above a gelatinized layer or directly on a non-gelatinized hypodermium or trama; the epicutis often partly covered by a velar layer, the whole cuticle (pellicle) often separable from the context of the pileus; lamellae thick, in youth often obtuse or canaliculate at the edge, neither free nor decurrent, broad; spore print pure white; spores, basidia and cystidia gigantic, spores globose or subglobose, smooth, or echinate (as in *Laccaria* and *Mycenella*), inamyloid, acyanophilic or partly with  $\pm$  cyanophilic, with often thickened but always continuous wall which in EM preparations shows a characteristic surface structure (Pl. 49, 55); basidia normal; cystidia broad; hymenophoral trama regular; stipe usually mostly white, often radicate (with a pseudorrhiza), with or without a veil, if veiled, the veil often double; context soft-fleshy, white, unchanging, consisting of hyphae which are inamyloid, with clamp connections, rarely without them.

**Development of the carpophores:** "Hemiangiocarpous". Angiocarp ranges from slightly paravelangiocarpous (*O. radicata*) to bivelangiocarpous (*M. mucida*); it is generally pileostipitocarpous (but perhaps stipitocarpous in *O. canarii*) but rather isocarpous in subgenus *Xerula*. Reijnders (personal communication) thinks that the pilosity of the latter originates from a transformation of the original universal veil. Further data on growth and sexuality of *O. mucida* see Semerdžieva & Musilek, *Ceská Mykologie* 23: 44-53. 1970).

**Area:** Tropics, subtropics and northern-temperate zones, not transgressing the northern and altitudinal limit of the area of *Fagus*.

**Limits:** This genus can be separated from all related genera by the characters indicated in the keys and the generic description. For further comments, see under *Mycenella*.

Kühner (1980) observes that the dermatocystidia (hairs) of *O. radicata* are binucleate whereas those of *O. longipes* have 12 to 40 nuclei. This re-enforces the status of *Xerula* as a separate taxon if, indeed, his observations are valid for all species entering the two subgenera. We are not prepared to follow Dörfelt who separates *Xerula* generically. This attitude is defensible if a very narrow genus concept is

applied. However, the characters invoked by him are either not fully applicable in all species known to me (characteristics of the epicutis), or insignificant (annulus), or inconstant (radicant stipe).

*State of knowledge:* All 12 species are completely known.

*Practical importance:* Some species may occasionally be mildly parasitic on trees weakened by other factors; in subgenus *Oudemansiella* all but two have been tested for edibility and have been found to be good palatable food. *O. mucida* contains an antibiotic substance (Musílek, Šašek, Černa, Semerdžieva & Vondracek 1969). *O. radicata* was once believed to have cancerostatic properties.

## SPECIES

Subgenus I. **Xerula** (R. Maire) Sing. (*Xerula* Maire ut genus). Stipe and/ or pileus pilose and spores smooth. Veil scarcely developed.

*Type species:* *X. longipes* (Bull. ex St-Amans) Maire.

*O. longipes* (Bull. ex St-Amans) Moser [Collybia, Kummer; Mucidula, Boursier; Xerula, Maire; Gymnopus pudens (Pers. ex) S.F. Gray; Xerula, Sing.]; *O. badia* (Quél.) Moser (Collybia longipes var. badia Quél.); *O. pilosa* (Rick) Sing. (Xerula, Sing.; Lentinus, Rick); *O. melanotricha* (Dörfelt) Moser; *O. americana* (Mitchel & A.H. Smith) Sing.\*; obviously also *O. renati* Clémençon, *O. caussei* (Mre) Moser apud Clémençon, and *O. xeruloides* Bon [the latter according to Dörfelt (1980) rather to (subgenus *Oudemansiella*)].

Subgenus II. **Oudemansiella**. Stipe not pilose, or spores echinate; setose, long dermatocystidoid hairs absent. Veil present or absent.

*Type species:* *O. platensis* (Speg.) Speg. [= *O. canarii* (Jungh.) Höhnel].

*O. mucida* (Schrader ex Fr.) Höhnel (Armillaria, Kummer; Collybia, Quél.; Lepiota, Schröter; Mucidula, Pat.); *O. canarii* (Jungh.) Höhnel [Hygrophorus variolosus Fr.; Collybia alphitophylla (Berk. & Curt.) S. Ito & Amai; Amanitopsis cubensis (Berk. & Curt.) Sacc.; Oudemansia platensis (Speg.) Speg.; Oudemansiella, Speg.; Armillaria cheimonophylla (Berk. & Curt.) Sacc.; Mucidula, Pat.; Phaeolimacium bulbosum Henn.; Pluteus macrosporus Henn.]; *O. linicolor* Grinling (ined.), as preceding species but pileus blue; *O. hygrophoroides* Sing. & Clémençon; *O. radicata* (Relh. ex Fr.) Sing. [Collybia, Quél.; Mucidula, Boursier; Clitocybe megalospora Clements; Hygrophorus gigasporus Cooke & Mass.; Agaricus alveolatus Kalchbr.; Agaricus megalus Pers.\*\*]; *O. steffenii* (Rick) Sing.

\*c.n. (*Oudemansiella longipes* var. *americana* Mitchel & A.H. Smith, *Mycologia* 70: 1045. 1978.)

\*\**O. radicata* should be split up into microspecies, one of which would be *Agaricus napipes* Hook. fil. (*A. olivaceoalbus* Cooke & Mass.), perhaps the same as *Oudemansiella ephippium* (Fr. sensu Ricken non Fr.) Moser. Another form which deserves consideration as a possible microspecies within the stirps *Radicata* is probably still unnamed; it is distinguished by globose spores and comes from New Zealand (also seen by Horak, *N.Z. J. Bot.* 9: 448 fig. 271. 1971). Still another form is the dry form, often observed by A.H. Smith in Michigan and by this writer in various regions of Europe and North and South America, recently named *Oudemansiella pseudoradicata* by Moser.

(*Tricholoma* Rick; *Oudemansiella echinosperma* Sing.); *O. macracantha* Sing. and *O. glutinosa* Sing. (ined.) with glutinous stipe; obviously also *O. kuehneri* (Romagnesi) Sing. (*Mycenella*, Romagnesi), *O. xeruloides* Bon, *O. nigra* Dörfelt and a related black South American species (ined.); perhaps also *Hygrophorus tesselatus* Heim.

## 77. MYCENELLA (Lange) Sing.

*Notulae Systematicae Sect. Crypt. Inst. Bot. Acad. Sc. U.S.S.R. fasc. 10-12: 9. 1938.*

*Type species: Mycena (Mycenella) margaritispora* Lange.

*Syn.: Mycena* subg. *Mycenella* Lange, *Dansk Bot. Ark.* 1(5): 16. 1914.

*Mycena* subg. *Paramycena-Hemimycena* sect. *Mycenella* Kühner, *Genre Mycena*, p. 609. 1938.  
*Marasmius* sect. *Laccariosporae* Sing. *Beih. Bot. Centralbl.*, Abt. B 56: 163. 1936.

**Characters:** Habit of the carpophores mycenoid to almost marasmoid but rather small (diameter usually not more than 20 mm), not pilose-hirsute but often pruinose or pubescent, dry sometimes slightly sticky, not glutinous, pigment usually present in pileus and stipe but not bright colored, usually gray or pale to dark fuscous or fuliginous or melleous; lamellae subfree to adnate, white to gray, horizontal or initially somewhat ascendant; epicutis consisting of diverticulate hyphae, not hymeniform, rarely with interspersed hairs; hypodermium without or with voluminous elements; hymenophoral trama regular to subirregular or subintermixed; spore print white to light cream color; spores small (to 9.5  $\mu\text{m}$ ), usually spiny, more rarely smooth, acyanophilic, with a very large hilar appendage; basidia without siderophilous granulation, normal in size for this tribus 2-spored or 4-spored, rarely 1-spored or 3-spored; cystidia present on the sides of the lamellae, rarely inconspicuous; spores and hyphae inamyloid; hyphae of stipe not metachromatic in cresyl blue mounts; clamp connections present or absent; plants often homothallic-diploid or parthenogenetic. On various dead and living parts of Cormophyta, or on humus.

*Development of the carpophores:* Unknown.

*Area:* The rough-spored group in the temperate zone but smooth-spored forms also in the American tropics and subtropics.

*Limits:* Romagnesi has pointed out that *Mycenella* and *Xerula* are closely related (*Bull. Soc. Myc. Fr.* 56: 59-65. 1940), in fact he thinks that these genera are not divided by a hiatus ("il n'y a aucune solution de continuité entre ces deux genres"), and that they should be combined under the name *Mycenella*. The hairy species with *Collybia*-habit with constantly smooth spores do not seem to be so inseparably linked with the small mycenoid species with echinate or small spores. It may be argued that the pilosity of the *Xerulas* is nothing but an extreme of the (microscopical) hairs observed in *Mycenella*, and it may be said that if smooth spores are admitted in *Mycenella* (*M. salicina*), echinate spores should also be admitted in the large-spored forms (*Xerula*). But since these characters coincide with the general habit of the carpophores, and therefore a correlation between two important

characters exists, whereby one of them is basic in the Friesian sense, the author thinks that at present the taxonomist cannot go beyond an acknowledgement of Romagnesi's demonstration of affinity between the genera *Mycenella* and *Xerula* (= *Oudemansiella*). They can be kept as separate genera and are obviously not as intimately related as the subgenera of *Oudemansiella* are related with each other. It may even be argued that *Mycenella* is closer to the Mycenae than to the Marasmieae.

It seems to this author, that the presumably intermediate species, *M. kuehneri* Romagnesi, can be presented as intermediate only as long as it is not recognized that *M. kuehneri* is by no means either *Mycenella* or *Oudemansiella* subgenus *Xerula*, but according to its spore characters which are practically identical with those of *O. steffenii*, a small *Oudemansiella* subgenus *Oudemansiella* with pilose dermatocystidia. What is really the question here, then, is the delimitation of the genus *Oudemansiella*, not that of *Mycenella*. Moser (1955) has drawn the consequence of this, disagreeing with Romagnesi as for the weakness of the limits of *Mycenella* but arguing in favor of cancellation of *Xerula* and its incorporation in *Oudemansiella*, a point of view accepted here as basically sound. Moser indicates his *O. pseudoradicata*, a not uncommon dry form near *O. radicata*, as an indubitable transition from *Oudemansiella* to *Xerula*. Another such transition is seen in *O. americana*, a fact recognized by Dörfelt (*Feddes Rep.* 92: 278-286. 1981). *Tricholomopsis platyphylla* cannot be indicated as such; the structure of the epicutis in *T. platyphylla* which is not hymeniform, the smaller spores (than in both *Oudemansiella* and *Xerula*) with weaker, acyanophilic walls, the absence of pleurocystidia and the entire habit prove that *T. platyphylla* is a *Tricholomopsis* - a fact which becomes much clearer to non-European mycologists who have studied other species but *T. rutilans* and *T. platyphylla* - and does not even come close to *Xerula* and *Oudemansiella*. The rest of the allegedly intermediate species are so incompletely known (if they exist) and their characters exclusively derived from literature interpretations that they cannot be given much value in this discussion. It is therefore evident that on the basis of the material presented, it is impossible to agree with Moser, neither as far as the gradual transition between *Oudemansiella* and *Xerula* is concerned, nor in regard to his transfer of *Tricholomopsis platyphylla* to *Oudemansiella*. Corner's (1966) statement that *Mycenella bryophila* is a "marasmoid ally of *Troglia* to which it may be reduced, and not nearly as related either to *Mycena* or to *Oudemansiella* both of which are monomicic" (instead of "sarcodimitic" in the terminology of Corner) disregards the findings indicated in the preceding paragraphs and is based exclusively on the hyphal structure of one species of *Mycenella*. If Corner's findings can be generalized, they would merely provide an additional distinctive character between *Oudemansiella* and *Mycenella*, and perhaps between *Mycena* and *Mycenella*. The affinity of *Mycenella* with *Troglia* is certainly not a close one.

*State of knowledge:* Ten species of *Mycenella* are now known, not counting the species that might be distinguished on the basis of differences in sexuality. These species can be considered as well known.

*Practical importance:* Some species may be mildly parasitic.

## SPECIES

### 1. Smooth-spored species:

*M. salicina* (Vel.) Sing.

### 2. Species with ornamented spores, verruculose or spinulose or punctate with heterogenous spore wall.

*M. margaritispora* (Lange) Sing.; *M. lasiosperma* (Bres.) Sing.; *M. bryophila* (Vogl.) Sing.; *M. cyatheae* (Sing.) Sing.; *M. fuliginosa* Sing.; *M. minima* Sing.; *M. cooliana* (Oort) Sing. (*Mycena trachyspora* Rea sensu A.H. Smith; sensu Rea = *Mycena olida* according to Orton); probably also *Mycena nodulosa* A.H. Smith.

## 78. PHYSOCYSTIDIUM Sing.

*Persoonia* 2: 410. 1962.

*Type species: P. cinnamomeum* (Dennis) Sing.

*Characters:* Habit of the carpophores collybioid; epicutis a trichodermial palisade consisting of erect, rather broad, not isodiametric, septate, parallel elements with intraparietal cinnamon pigment, without dermatocystidia, not hymeniform, without broom cells of any kind and without *Rameales*-structure or asterostromelloid structure; thin-walled pleurocystidia present; spores smooth, rather small, ellipsoid, inamyloid, white in print; hyphae of the trama with clamp connections, inamyloid; hymenophoral trama regular; pseudorrhiza absent; pileus not glutinous but velutinous; stipe hollow, not insititious, central; veil absent. Lignicolous, tropical.

*Development of the carpophores:* Unknown.

*Area:* Neotropics (Trinidad).

*Limits:* The trichodermial palisade of this species is quite different from the trichodermium sometimes observed in the Collybieae, as for example in *Troglia* which is very different in appearance. Among the Marasmieae, the genus is well characterized by the key characters.

*State of knowledge:* The only species known has been studied thoroughly except for culture and development characters.

*Practical importance:* Unknown.

## SPECIES

*P. cinnamomeum* (Dennis) Sing.

## 79. STROBILURUS Sing.

*Persoonia* 2: 409. 1962.

*Type species: S. conigenoides* (Ellis) Sing.

**Characters:** Habit collybioid; epicutis hymeniform; dermatocystidia present in the cortical layers of the pileus and stipe; muricate cystidia (with excretive function: pseudocystidia) present as pleuro- and cheilocystidia; spores inamyloid, acyanophilic, hyaline, smooth, with homogenous wall, small to medium sized, ellipsoid to oblong, not broader than 4.5  $\mu\text{m}$  hyphae inamyloid, without clamp connections, not gelatinized; pigment present or absent; hymenophoral trama regular, often of the *Clitocybe*-subtype, but never truly bilateral (excepting the primordia); pseudorrhiza present, rising from cones of conifers and inflorescences of Magnoliaceae rarely passing onto other woody substrata; pileus not glutinous; veil none.

*Development of the carpophores:* Unknown.

*Area:* Circumpolar on the Northern Hemisphere, south to Central America and South Africa.

*Limits:* The characters of the spores and the absence of clamp connections as well as the pseudorrhiza and habitat characterize this genus. It differs from *Marasmius* sect. *Alliati* in the absence of clamp connections. The hymenophoral trama is of very different structure when compared with that of the genus *Pseudohiatula* with which it had been classified.

*State of knowledge:* The seven species of this genus known to this author and enumerated below are well known except for the development of the carpophores. See also Singer, *Persoonia l.c.* and Kalamees, *Trans. Tartu State Univ.* 268: 373-404. 1970. An excellent monograph of the American species was published by Redhead (*Can. J. Bot.* 58: 68-83. 1980).

*Practical importance:* Some species are edible. Marasmic acid, an antibacterial substance isolated from *S. conigenus*, was indicated by Kavanagh et al. (*Proc. Nat. Acad. Sc. Washington* 53: 343. 1949). Strobilurins, antifungal substances, have been isolated from *S. tenacellus*; these are probably important in phytopathology (control of *Botrytis cinerea*, *Rhizoctonia solani* etc.), see Anke, *Zeitschr. f. Mykologie* 44: 133. 1978 where reference is made to an earlier paper (Anke, Oberwinkler, Steglich & Schramm, *J. Antibiot.* 30: 806-810. 1977) which indicates that strobilurin also showed a distinct anti-tumor activity.

### SPECIES

*S. conigenoides* (Ellis) Sing.; *S. esculentus* (Wulf. apud Jacquin ex Fr.) Sing. with var. *montezumae* Sing.; *S. stephanocystis* (Hora) Sing. (*Marasmius conigenus* (Pers.) ex Fr.) Karst. (sensu Pat.; sensu Kummer, Ricken = *S. esculentus*; sensu Bres. = *S. tenacellus*; sensu Lange = *Baeospora myosura*, (according to Orton); S.

*tenacellus* (Pers. ex Fr.) Sing.; *S. albipilatus* (Peck) Wells & Kempton (Collybia, Peck; Marasmius, Sing.; *S. lignatilis* Wells & Kempton); *S. occidentalis* Wells & Kempton; *S. trullisatus* (Murr.) Lennox.

### Subtribus *Marasmiinae* Sing.

*Lilloa* 22: 317. 1949 (publ. 1951).

Type genus: *Marasmius* Fr.

**Characters:** Habit collybioid (marasmoid), almost mycenoid, pleurotoid, or cyphelloid, often spatulate, rarely in form of a stipitate hollow head; hymenophore present and then in form of lamellae (which may be anastomosing or intervenose) or veins, or absent; stipe sometimes seta-like and dark, often insititious, sometimes rising from black rhizomorphs; epicutis hymeniform, more rarely with broom cells not hymeniformly organized (and then stipe seta-like and dark, insititious, or carpophore spatuloid with smooth hymenial surface), or absent from the pileus (which is then completely covered by a fertile hymenium), broom cells and/or dermatocystidia often present; basidioles generally fusoid; cystidia and pseudocystidia present or absent in the hymenium; cheilocystidia mostly present if a hymenophore is developed, and then often like the elements of the epicutis; pseudorrhiza rarely present; veil none; hyphae of the pileus and stipe either both or only those of the stipe pseudoamyloid, or both in pileus and stipe inamyloid; carpophores frequently (but not always) reviving after drying out when remoistened, rarely fleshy-putrescent; spores white or pale cream in print, of various shapes, hyaline (KOH), thin-walled, with inamyloid, acyanophilic or cyanophilic smooth, homogenous wall, small to gigantic. On various plant débris, in the litter, also on living plants, or on earth.

## 80. MARASMIUS Fr.

Gen. Hymen., p. 9. 1836.

Type species: *M. rotula* (Scop. ex Fr.) Fr.

Syn.: *Heliomycetes* Lév., Ann. Sc. Nat. III. 2: 117. 1844 (typus: *H. elegans* Lév.).

*Androsaceus* (Pers.) Pat., Hymen. Eur., p. 105. 1887 (typus: *M. rotula* (Scop. ex Fr.) Fr.).

*Chamaeceras* Reb. ex O. kuntze, Rev. Gen. Pl. 3, 2: 454. 1898 (typus: *M. androsaceus* (L. ex Fr.) Fr., according to Donk not validly published).

*Mycenitis* Earle, Bull. N. Y. Bot. Gard. 5: 414. 1909 (variant spellings *Mycetinis*, *Mycetinus*) (typus: *M. alliaceus* (Jacq. ex Fr.) Fr.).

*Marasmius* subgen. *Collybiopsis* Schröter in Cohn, Fl. Schles. 3, 1: 559. 1889 (typus: *Agaricus calopus* Pers. ex Fr.\*).

\*I consider *M. calopus* a fungus close to *M. scorodonius*, at least in the original sense, cf. Beih. Nov. Hedwigia 40: 316. 1973; Orton disagrees (1960). Earle (1909), Horak (1968), and Kühner (1980) are certainly mistaken considering *A. ramealis* the type because this species is not included in the basionym (as well as for other reasons).

*Collybiopsis* (Schröt. in Cohn) Earle, *Bull. N. Y. Bot. Gard.* 5: 415. 1909 (typus: *A. calopus* Pers. ex Fr.).

*Tephrophana* Earle, l.c., p. 427 (typus: *M. albogriseus* (Peck) Sing. \*).

*Scorteus* Earle, l.c., p. 415. (typus: *M. oreades* (Bolt. ex Fr.) Fr.).

*Polymarasmius* Murr., *N. Am. Flora* 9: 286. 1915 (typus: *M. multiceps* Berk. & Curt.).

?*Vanromburghia* Holtermann, *Myc. Untersuchungen Trop.*, p. 104. 1898 (typus: *V. silvestris* Holtermann (see also p. 855)).

**Characters:** Habit collybioid (to almost mycenoid) or pleurotoid, mostly somewhat toughish and reviving after drying out when remoistened; hymenophore lamellate, rarely smooth or venose for a long time but eventually mostly becoming lamellate, lamellae sometimes intervenose or anastomosing; epicutis either hymeniform or not, if not, consisting of broom cells or at any rate strongly diverticulate-nodulose hyphal elements (and then either the whole trama or only that of the stipe more or less distinctly pseudoamyloid or at least the stipe seta-like and shining-blackish and insititious, or absent to small and eccentric to lateral); trama of the pileus monomitic, pseudoamyloid or inamyloid; no gelatinous layers; clamp connections present or more rarely absent, if absent - epicutis with broom cells. Black rhizomorphs often present, sometimes stipe of carpophore rising from it; telepods often formed; if there is a basal mycelium, the epicutis is always hymeniform; some species form endotrophic mycorrhiza, none ectotrophs or lichens. Most frequently on wood or leaves, dead or living, more rarely on other kinds of litter, among moss or on the earth among grasses, but often on roots or leaves of living or dead Gramineae.

**Development of the carpophores:** At least in a few species paravelangiocarpous, and pileostipiticarpous (in *M. rotula*, *bulliardii*, *wynnei*, and *pahouinensis*). However some species e.gr. *M. floriceps* seem to be gymnocarpous according to the present author's observations.

**Area:** Almost cosmopolitan, but much more numerous and more species in the tropical regions than in the temperate and frigid ones.

**Limits:** The limits with the other genera enumerated under no. 81-88 will be pointed out under these genera. At times there is a difficulty in delimiting *Marasmius* sect. *Androsacei* from *Marasmiellus* sect. *Rameales*, but the stiff, horse hair-like stipe, often shining and glabrous, or itself beset by seta-like bodies, often rising from or accompanied by black rhizomorphs, the occasional garlic odor, the complete absence of mycelium at the base of the fully insititious stipe, the mostly distinct pseudoamyloid hyphae (at least in the rind of the stipe) and the precise structure of the cheilocystidia and elements of the epicutis - difficult to describe in a generalized way for comparison with *Marasmiellus* - and the general aspect are usually sufficient indications as for the generic identity of a species. The modern differentiation and separation between *Marasmius* and *Collybia* goes back to Singer (1936 - *Beih. Bot. Centralbl.* 56: 157) and does not present any difficulties even now that many more species are known in both genera.

*Strobilurus* differs from *Marasmius* section *Alliacei* in the absence of clamp

\* Unlike *Collybiopsis* (Schröt.) Earle, this genus has no basionym and is only said to be "equivalent" to a Friesian section. Donk (1962) was therefore correct in the lectotype designation in both cases.

connections from sect. *Inaequales* in the absence of broom cells. - *Oudemansiella* differs from sect. *Alliacei* in often more voluminous or broader spores; many species are viscid, and most have a pseudorrhiza. Those Oudemansiellas which are not viscid can still be distinguished by size of the dermatocystidia, the positive cyanophily of the outermost spore layer, and the pseudorrhiza. *Physocystidium* differs from the *Alliacei* in the peculiar epicutis structure.

Those genera of Myceneae which have inamyloid spores differ from *Marasmius* by not having a hymeniform layer on the pileus and not being insititious with a tough blackish stipe, or by being strictly fleshy-membranous and putrescent-non-reviving, and at the same time mycenoid.

It is always important to compare the genera of Pseudohiatuleae, especially if the epicuticular layer is non-hymeniform or devoid of broom cells. If a stage corresponding to the young carpophore just before sporulation is not at hand, there may be confusion about the bilaterality of the hymenophoral trama.

As for *Vanromburghia*, see under that genus on p. 855.

Some species of *Hydropus* which have inamyloid spores differ from the Marasmii with non-insititious stipe in hyphal shapes and pigments (see under *Hydropus*).

Kühner (1980) describes the family Marasmiaceae based on *Marasmius* as having "stipes centralis". The pleurotoid Marasmii would apparently be excluded, but since *Chaetocalathus*, also pleurotoid, is included in *Crinipellis* (Marasmiaceae), this is probably only an oversight.

*State of knowledge:* *Marasmius* is a very large genus in which I now recognize 356 species. The South American and neotropical Marasmii have been monographed (Singer 1976); so have been those of the Congo (Singer 1964). There has not been a recent monograph of the European species, but Kühner's (1934) papers are still excellent and provide most of the data needed. The monograph by Petch (1947) does not provide any dependable anatomical and microchemical data but still gives a useful account of the Marasmii of Ceylon; those of Central and East Asia as well as Western North America have been studied less thoroughly and certainly never monographically. The Eastern North American species were monographed by Gilliam (1976); the Australian, New Zealand, and tropical African (outside Zaire). Marasmii have only been studied as far as some modern authors (Heim, Pegler, Horak) have commented on them. See Pl. 59, 60, 63, 1 g.

*Practical importance:* Some species have some importance causing disease of tropical crops such as tea, sugar cane, coffee, *Hevea*. This involves particularly such species as *M. crinisequi*, *M. viegasii*, *M. cyphella*; many diseases have been related to *Marasmius* in the wider sense, but should now be classified under *Marasmiellus* and *Crinipellis*. *M. oreades* seems to damage lawns and pastures, since its influence on the growth rate and quality of the grass and other herbaceous vegetation is negative, i.e. its presence is undesirable in spite of the fact that the plants in immediate reach of the "fairy rings" appear to be better developed, deeper green (more nitrogen available) and faster-growing than in absence of the fungus. *M. oreades* is also a valuable edible fungus of more than local importance since it is

exceedingly common, even in urban habitats and well known under a number of vernacular names in several continents. It can rather easily be grown (cf. Singer, *Mushrooms and Truffles*, p. 168, pl. 1, 1961). *M. albogriseus* is commonly eaten in the Department of Cuzco, Perú, and *M. buzungolo* and *piperodorus* are collected for food and sold in the markets of the Zaire Republic (ex Belgian Congo). Several other species are edible but little known (*M. pampicola*, *collinus*, and others), but *M. scorodonius* can be used as condiment for soups, sauces, etc. in French cuisine (it has garlic flavor). Some of the species which produce extensive black rhizomorphs, especially forms like *M. crinisequi* have been and probably still are used by the peoples of East India, Indonesia, and the Congo to tie jewelry. Some birds use these rhizomorphs extensively to build their nests (see H. Sick, *Journ. f. Ornithol.* 98(4): 421-431. 1959), but can be tempted to use man-made wire instead.

## SPECIES\*

Sect. 1. *ANDROSACEI* Kühn (1933). In contrast to the other sections of the genus, the epicutis is here (and in *Fusicystides*) not hymeniform, but consisting of irregular broom cells and diverticulate hyphae; stipe thin and bristle-like, usually, at least in age, nearly or quite black and often shiny, reminding one of horse hair, central, insititious; lamellae varying from subfree to decurrent to collariate or none; trama of the pileus rarely, of the stipe mostly pseudoamyloid; clamp connections present or absent; spores acyanophilous. Both tropical and extra-tropical.

\*Kühner's classification has been proposed without due regard to the conservation of published sectional names. He did not take advantage of the names already published as sectional names in the genus *Marasmius*. Fries divides the genus *Marasmius* in two subgenera, *Collybia* Fr. and *Mycena* Fr., and each of these is subdivided into sections. In order to preserve Kühner's names - which the author considers desirable - it had to be proposed (Singer 1951, 1962) that the lectotypes of the Friesian sections and subsections (originally tribus and subtribus) are admitted in the following manner:

*Collybiae* Fr. ex Quél.: *M. peronatus*, thus a synonym of *Vestipedes*.

*Scortei* (Fr. "subtribus") Quél. (subsection) is a subdivision of *Vestipedes* = *Collybiae*, again with *M. peronatus* as type.

*Tergini* (Fr. "subtribus") Quél.: *M. fuscopurpureus*.

(Both *M. peronatus* and *M. fuscopurpureus* are here transferred to *Collybia*).

*Chordales* Fr. (subtribus), if it should be taken up as a section, it would be typified by *M. caudicinalis* (proposed as lectotype by me in 1951 which would make it a synonym of *Xeromphalina* subgen. *Xeromphalina*).

*Mycenae* (Fr.) ex Quél.: *M. rotula* (thus a synonym of sect. *Marasmius*).

*Rotula(e)*: *M. rotula*, thus a synonym of sect. *Marasmius*.

*Stipitarii* (Fr. ("subtribus")) if used as a section: *A. stipitarius* (which makes it a synonym of *Crinipellis* sect. *Crinipellis*).

*Calopodes* (Fr., subtribus of *Collybia*), if used as a section: *A. calopus* (this is a *nomen dubium* or an older name for *Alliacei*).

Whether Berkeley's "divisions" [*Scortei* (Fr.) and *Chondropodes* (Fr.)] can be taken as equivalents of sections, remains improbable but, if admitted, these names would supersede the established section *Vestipedes* and *Striipedes* of *Collybia*.

Type species: *M. androsaceus* (L. ex Fr.) Fr.

*M. androsaceus* (L. ex Fr.) Fr.; *M. splachnoides* Fr.; *M. polylepidis* Dennis in Sing.; *M. pilgerodendri* Sing.; *M. flotowiophilus* Sing.; *M. hyalinotrichus* Sing.; *M. bactrosporus* Sing.; *M. hakgalensis* Petch; *M. polychaetopus* Sing.; *M. dysodes* Sing.; *M. aporophyphes* Sing.; *M. kisangensis* Sing.; *M. lomatiae* Sing.; *M. defibulatus* Sing.; *M. pacificus* Sing.; *M. aporus* Sing.; *M. yalae* Sing.; *M. cyrillidis* Dennis; *M. leguminosarum* Sing.; *M. earlei* Murr.; *M. liquidambari* Sing.; *M. cryptotrichus* Sing.; *M. chiapasensis* Sing.; *M. radicellicola* Sing.; *M. atroin-crustatus* Sing.; *M. atlanticus* Sing.; *M. perreductus* Sing.; *M. tomentellus* Berk. & Curt.

Sect. 2. *HYGROMETRICI* Kühner (1933). Pileus usually well pigmented; epicutis formed by broom cells of the *Rotalis* type which form, at least in portions of the pileus, a hymeniform layer, some of the cells often smooth but never all of them; spores medium sized to large; stipe insititious, thin dark, at least at the base, glabrous or beset with setae, simple, central; lamellae well formed, neither venose, nor collariate; black rhizomorphs at times present; trama not pseudoamyloid; odor none; on dead vegetable matter.

Type species: *Marasmius hygrometricus* (Brig.) Sacc.

*M. buxi* Fr. in Quél.; *M. hudsonii* (Pers. ex) Fr.; *M. corbariensis* (Roumeguère) Sing. (*M. hygrometricus* (Brig.) Sacc.; *M. olivetorum* Mont. & Fr.); *M. ilicis* Sing.; *M. minutus* Peck (*M. capillipes* Sacc.); *M. crescentiae* Murr.; *M. sphaerodermus* Speg.; *M. echinosphaerus* Sing.; *M. magnoliae* Sing.; *M. actiniceps* (Kalchbr. & Cooke) Reid (*Mycena*, Sacc.); *M. kroumirensis* (Pat.) Sacc. & Syd. *M. exustus* Berk. & Curt.

Sect. 3. *LEVEILLEANI* Sing. (1964). Pileus medium sized to rather large (9-39 mm broad), usually well pigmented, with an epicutis consisting of a hymeniform layer with smooth, ventricose to clavate elements, some of which show finger-like, mostly apical outgrowths or low processes; spores medium sized; lamellae free but not collariate; hyphae with clamp connections, inamyloid; stipe central, insititious; cystidia none on the sides of the lamellae. Tropical.

Type species: *M. leveilleanus* (Berk.) Pat.

*M. leveilleanus* (Berk.) Pat.; apparently also *M. bubalinus* Pegler.

Sect. 4. *SCOTOPHYSINI* Sing. (1962). Pileus pigmented, with a hymeniform epicutis consisting of globose pedicellate elements which are smooth; cystidia none; cheilocystidia corn-cob to cauliflower-like; hypodermium with incrusting membrana pigment; spores oblong to subcylindric; lamellae not collariate; stipe black, insititious, central, long, setose; hyphae inamyloid, with clamp connections; context inodorous. On dead leaves. Tropical.

Type and only known species: *M. scotophysinus* Sing.

Sect. 5. *EPIPHYLLI* Kühner (1933). Pileus white or whitish sometimes eventually light yellowish pink with hymeniform epicutis consisting of smooth, exceptionally also diverticulate short elements interspersed with or devoid of dermatocystidia (but

if dermatocystidia are present on the pileus, they are neither pseudoamyloid nor capitate), without long, bristle-like hairs; spores narrowly cylindric to oblong or ellipsoid, small to large; lamellae subfree to subdecurrent, neither collariate nor subcollariate; hyphae with or without clamp connections, inamyloid or pseudoamyloid (but if pseudoamyloid - epicuticular elements always smooth); stipe central or eccentric, attached to leaves or more rarely to wood or to rhizomorphs or telepods by an insititious base; cystidia on the sides of the lamellae present but sometimes very scattered and inconspicuous (looking much like the basidioles), mostly fusoid to ampullaceous, rarely vesiculose, generally thin-walled and hyaline, but may have pigmented resinous incrustation; stipe with conspicuous hairs or dermatocystidia. Both tropical and extratropical.

*Type species: M. epiphyllus* (Pers. ex Fr.) Fr.

Subsection *Epiphyllini* Sing. (1962). Tramal hyphae, at least in the apex of the stipe, inamyloid, epicuticular cells weakly diverticulate-uneven, or smooth; hymenophore veined radially, meruliod, or lamellate, sometimes almost absent especially in young (but already fertile) specimens.

*Type species: N. epiphyllus* (Pers. ex Fr.) Fr.

*M. epiphyllus* (Pers. ex Fr.) Fr.\*; *M. tenuiparietalis* Sing.; *M. martini* Sing. (*Cymatella longipes* Martin); *M. euosmus* Sing.; *M. carpenterianus* Sing.; *M. felix* Morgan; *M. munyozi* Sing.; *M. exiguum* Sing.; *M. hemimycena* Sing.; *M. plantaginis* (Heim "plantaginae") Sing.\*\*; *M. tremulae* Velen.;

Subsect. *Eufoliatini* Sing. (1962). Hyphae of the trama - at least in the stipe - distinctly pseudoamyloid. Lamellae well formed but sometimes forked or eventually intervenose or anstomosing.

*Type species: M. eufoliatus* Kühner.

*M. recubans* Quél. (*M. eufoliatus* Kühner); *M. sanctixerii* Sing.; *M. caliensis* Sing. also a minute species from Central Asia (ined.).

Subsect. *Epiphyolloidei* Sing. (1973). As subsect. *Epiphyllini*, but epicuticular elements diverticulate.

*Type species* (only species known): *M. epiphyloides* Rea.

Sect. 6. *MARASMIUS* (sect. *Rotulae* (Pers. ex St. Amans) Fr.; *Collariati* Bat.; *Pararotulae* Sing.). Pileus mostly small, white or variously pigmented; often with a central knob or papilla in the middle which at maturity is often located in an umbilicus and surrounded by a pallid ring-zone, or merely a dark dot present instead of the papilla; epicutis hymeniform (but may in the end become slightly

\*Neotype Singer C 4130 (BAFC) from Ulfält, N of Femsjö, 19 VIII 1964. This is "*A. epiphyllus* Pers. ad part." Fr. Syst. 1: 139. 1821, also described from the Femsjö region in Sweden, with thick-walled hymenial elements of the epicutis. The following species (*M. tenuiparietalis* Sing.) is often confused with *M. epiphyllus*.

\*\*st.n. (*Androsaceus epiphyllus* var. *plantaginea* Heim, Treb. Mus. Cienc. Nat. Barcelona 15 ser. 3: 89. 1934 = Petrak, Just's Bot. Jahr. 63: 812, 1935).

disorganized), consisting of broom cells, without long conspicuous hairs; spores small to large, ellipsoid to oblong; lamellae subcollariate to mostly distinctly collariate, rarely absent to reniform; hyphae with clamp connections, mostly at least in the apex of the stipe distinctly pseudoamyloid, more rarely all (nearly) inamyloid; stipe central, insititious, attached to black rhizomorphs or directly to the substratum (leaves, wood); cystidia none, rarely present and very inconspicuous, but cheilocystidia generally present, and mostly like the epicuticular broom cells, sometimes pigmented; rhizomorphs (black) often accompanying the carpophores, glabrous, in a few species pilose.

*Type species: M. rotula* (Scop. ex Fr.) Fr.

Subsection *Pararotulae* (Sing.) Sing. (1975). Epicutis with broom cells of the Rotalis type (with divergent setulae).

*Type species: M. pararotula* Sing.

*M. multiceps* Berk. & Curt. (*M. submulticeps* (Murr.) Sacc. & Trotter); *M. griseolofuscescens* Sing.; *M. cupressiformis* Berk.; *M. rotuloides* Dennis; *M. panamensis* Sing.; *M. vergeliensis* Sing.; *M. castellanoi* Sing.; *M. pararotula* Sing.; *M. limosus* Quél.; *M. bulliardii* Quél.; *M. rotula* (Scop. ex Fr.) Fr.; *M. pandoanus* Sing.; *M. oaxacanus* Sing.; *M. manuriensis* Sing.; *M. psychotriophilus* Sing.; *M. cundinamarcae* Sing.; *M. leucorotalis* Sing.; *M. arimanus* Dennis; *M. idroboi* Sing.; *M. scototephrodes* Sing.; *M. leucozonitiformis* Sing.; *M. carminis* Sing.; *M. carneotinctus* Sing.; *M. tanyspermus* Sing.; *M. violeorotalis* Sing.; *M. buzae* Dennis; *M. populiformis* Berk.; *M. minimus* Dennis; *M. nothomyrciae* Sing.; *M. dodecaphyllus* Sing.; *M. platyspermus* Sing. in Sing. & Digilio; *M. nebularum* Sing.; *M. aequatorialis* Sing.; *M. hylaeicola* Sing.; *M. austrorotula* Sing.; *M. baumannii* Henn.; *B. rotalis* Berk. & Br.; *M. apatelius* Sing.; *M. pluvialis* Sing.; *vigintifolius* Sing.; *M. idroboi* Sing.; *M. eucladopus* Sing.; *M. tetrachroinus* Sing.; *M. tereticeps* Sing.; *M. variabiliceps* Sing.; *M. louisii* Sing.; *M. capillaris* Morgan.; *M. baeocephalus* Sing.

Subsection *Penicillati* Sing. (1973). Broom cells of the Siccus-type.

*Type species: M. graminum* (Lib.) Berk.

*M. peckii* Murr.; *M. conicopapillatus* Henn.; *M. pallenticeps* Sing.; *M. aspilocephalus* Sing.; *M. chrysochaetes* Berk. & Curt.; *M. nigrobrunneus* (Pat.) Sacc. (*M. griseiolaceus* Petch); *M. fuligineorotula* Sing.; *M. magnisetulosus* Sing.; *M. misionensis* Sing.; *M. schultesii* Sing.; *M. trichorhizus* Speg.; *M. conquistensis* Sing.; *M. boliviæ* Sing.; *M. pallipes* Speg.; *M. aciculaeformis* Berk. & Curt.; *M. polycladus* Mont.; *M. rubromarginatus* Dennis; *M. marthae* Sing.; *M. sanguirootalis* Sing.; *M. microdendron* Sing.; *M. hippiochaetes* Berk.; *M. xerampalinus* Sing.; *M. hiorami* Murr.; *M. aripoensis* (Dennis) Sing.; *M. edwallianus* Henn.; *M. puttemansii* Henn.; *M. megalospermus* Sing.; *M. chrysocephalus* Sing.; *M. xerophyticus* Sing.; *M. guyanensis* Mont.; *M. robertsonii* Sing.; *M. crinisequi* Müller ex Kalchbr. (*M. equicrinis* Müller apud Bark.); *M. dicotyledoneus* (Sing.) Sing.; *M. graminum* (Lib.) Berk.; *M. ruforotula* Sing.; *M. subruforotula* Sing.; *M. rufomarginatus* Sing.; *M. praecox* Sing.; *M. rhizomorphogeton* (Sing.) Sing.; *M. brunneocinctus* Sing.; *M. pallidocinctus* Sing.; *M. foliicola* Sing.; *M. subrhodocephalus* Henn.; *M.*

*beelianus* Sing.; *M. valdivianus* Sing.; *M. yangambensis* Sing.; *M. bromeliacearum* Sing.

Hymenophore absent or veniform: *M. apogonus* Sing.

Subsection *Horriduli* Sing. subsect. nov.\*. Differs from the preceding subsection in the presence of numerous pseudoamyloid setiform hairs, especially long at the margin of the pileus. Neotropical.

Type and only known species: *M. horridulus* Sing.\*\*

Sect. 7. *SICCI* Sing. (1958). Small to large carpophores with poorly to strongly developed but always demonstrable basal mycelium (fibrils, tomentum, strigosity), rarely with white rhizomorphs, never truly insidious in all carpophores of a population; context pseudoamyloid, with clamp connections; epicuticular elements in hymeniform arrangements and at least a large part of them in form of broom cells (of the Siccus-type). On wood, humus, leaves, culms, fruit, roots, living or dead, mostly saprophytically, more rarely endomycorrhizally or parasitically; spores small to more often medium to large, if large usually oblong-fusiform and relatively narrow. Seta-like hymenial and dermatocystidia often present, pleurocystidia present or absent; cheilocystidia mostly in form of broom cells, sometimes pigmented. Most species tropical.

Series *Leonini* Sing. (1976). Setiform elements none on pileus, stipe, and hymenophore. Cystidia on the sides of the lamellae absent or not clearly differentiated.

Type species: *M. leoninus* Berk.

*M. subrotula* Murr.; *M. helvoloides* Sing.; *M. haediniformis* Sing.; *M. subarborescens* Sing.; *M. bellus* Berk.; *M. xestocephalus* Sing.; *M. luteofuscus* Berk. & Curt.; *M. microhaedinus* Sing.; *M. beniensis* Sing.; *M. cuatrecasasii* Sing.; *M. proletarius* Berk. & Curt.; *M. amazonicus* Sing.; *M. tucumanus* Sing.; *M. tageticolor* Berk.; *M. ruber* Sing.; *M. ater* Sing.; *M. megistus* Sing.; *M. poecilus* Berk.; *M. phaeus* Berk. & Curt.; *M. bambusiformis* Sing.; *M. mazatecus* Sing.; *M. fulvoferrugineus* Gilliam; *M. borealis* Gilliam; *M. longisporus* (Pat. & Gaillard) Sacc.; *M. lilacinoalbus* Beeli; *M. rubricosus* Mont.; *M. rhabarberinus* Berk.; *M. graminicola* Spieg.; *M. sierraleonis* Beeli (*M. congoensis* (Beeli) Sing.); *M. carcharias* Sing.; *M. macrolobieti* Sing.; *M. floriceps* Berk. & Curt.; *M. berteroii* (Lév.) Murr.; *M. onoticus* Sing.; *M. convoluticeps* Sing.; *M. matrisdei* Sing.; *M. neglectus* Sing.; *M. corrugatus* (Pat.) Sacc. & Sydow; *M. bezerrae* Sing.; *M. pusio* Berk. & Curt.; *M. leoninus* Berk.; *M. napoensis* Sing.; *M. corrugatiformis* Sing.; *M. episemus* Sing.; *M. ochropus* Sing.; *M. piperodorus* Beeli; *M. katangensis* Sing.; *M. buzungulo* Sing.; *M. leptus* Sing.; *M. pulcherripes* Peck; *M. plicatulus* Peck; *M. epelaeus* Sing.; *M. trinitatis* Dennis; *M. digilioi* Sing. in Sing. & Digilio; *M. olivascenticeps* Sing.; *M. cladophyllus* Berk.; *M. araucariae* Sing.; apparently also *M. nodulocystis* Pegler.

\*Crinibus pseudoamyloideis setiformibus in epicute et praecipue in margine pilei numerosis. Typus: *M. horridulus* Sing.

\*\*Characteribus subsectionis Horridulorum gaudens. Ad folia in Brasilia Amazonica. Typus (Singer B 11272 (INPA).

Series *Haematocephali* Sing. (1976). Differs from the preceding series in the presence of pleurocystidia.

Type species: *M. haematocephalus* (Mont.) Fr.

*M. setulifolius* Sing.; *M. pleuracanthus* Sing.; *M. silvestris* Sing.; *M. megistosporus* Sing.; *M. pallescens* Murr.; *M. panerythrus* Sing.; *M. haematocephalus* (Mont.) Sing. (*M. rhodocephalus* Fr. non sensu Pat.; *M. semipellucidus* Berk. & Br.; *M. sanguineus* Cooke & Mass.; *M. atropurpureus* Murr.; *M. vinosus* Beeli); *M. litoralis* Quél.; *M. haedinus* Berk.; *M. splitgerberi* (Mont.) Sing.; *M. delectans* Morgan; *M. spegazzinii* Sacc. & Sydow; *M. praeandinus* Sing.; *M. yarizae* Sing.; *M. hylaeae* Sing.; *M. confertus* Berk. & Br. (*M. chondripes* Berk. and *M. hemibaphus* Berk. & Br. sec. Petch); *M. glabellus* Peck; *M. aztecus* Sing.; *M. pseudocorrugatus* Sing.; *M. dennisii* Sing.; *M. nogalesii* Sing.; *M. hinnuleus* Berk. & Curt.; *M. bambusinus* (Fr.) Fr.; *M. anomalus* Lasch in Rab. in Klotzsch; *M. ferrugineus* (Berk.) Berk. & Curt.; *M. wilsonii* Murr.; *M. phaeocystis* Sing.; *M. strigipes* Beeli; *M. elaeocephalus* Sing.; *M. hypophaeus* Berk. & Curt.; *M. guzmanianus* Sing.; *M. helvolus* Berk.; *M. tenuisetulosus* (Sing.) Sing.; *M. montagneanus* Sing.; *M. siccus* (Schwein.) Fr.; *M. virginianus* Sing.; *M. oleiger* Sing.; *M. allocystis* Sing.; *M. musicola* Murr.; *M. grandisetulosus* Sing.

Series *Actinopodes* Sing. (1976). Setiform dermatocystidia present on pileus and/or stipe distinctly pubescent, pruinose or hirsute from dermatocystoid hairs. First two species probably closer to Leonini.

Type species: *M. actinopus* Mont.

*M. chrysoblepharis* Sing.; *M. personatus* Berk. & Curt.; *M. spiculosus* Sing.; *M. fulvovelutinus* Beeli; *M. cohaerens* (A. & S. ex Fr.) Cooke & Quél.; *M. flammans* Berk.; *M. echinatulus* Sing.; *M. umbrinus* Pegler; *M. venezuelanus* Dennis; *M. jalapensis* Murr.; *M. rubroflavus* (Theissen) Sing.; *M. glaucopus* (Pat.) Sacc.; *M. afrosulphureus* Courtecuisse; *M. bahamensis* Murr.; *M. actinopus* Mont.; *M. atrorubens* (Berk.) Berk. (*M. castaneus* Mont.; *M. jamaicensis* Murr.; *M. portoricensis* Murr.); *M. pseudoniveus* Sing. with var. *amylocystis* Sing.; *M. heterocheilus* Sing.; apparently by also *M. mengoensis* Pegler (with gloecystidia!).

Sect. 8. *INAEQUALES* (Sing.) Sing. (st. n., sect. *Sicci* subsection *Inaequales* Sing. *Sydowia* 12: 97. 1959). As section 7, but with inamyloid trama.

This section is intermediate between sect. *Sicci* and sect. *Alliacei*.

Type species: *M. inaequalis* Berk. & Curt.

*M. inaequalis* Berk. & Curt.; perhaps here the Mediterranean *M. ventallonii* Sing. (green stipe) and *M. flavomerulinus* Redhead (without clamp connections, may be type of a special subsection, *Flavomerulini* ined.).

Sect. 9. *FUSICYSTIDES* Sing. in Sing. & Digilio (1951). Pileus eventually pigmented, with an epicutis of the type common in *Marasmiellus* sect. *Rameales* (often poorly developed), never hymeniform; cystidia conspicuous, incrusted; spores large, oblong, *Fusarium*-shaped or clavate or fusoid; lamellae not collariate; stipe somewhat mycelioid at base, oblique and eccentric, lateral or rudimentary, thus

habit pleurotoid; black rhizomorphs absent; hyphae partially weakly to strongly pseudoamyloid, with clamp connections; odor none. On dead wood.

Type species: *M. fusicystis* Sing. in Sing. & Digilio.

*M. isabellinus* Pat. (*M. fusicystis* Sing. in Sing. & Digilio); *M. campanella* Holtermann (*M. rufescens* Berk. & Br. (?)) according to Petch).

Sect. 10. *NEOSESSILES* Sing. (1958). Pileus pigmented or not, with epicuticular broom cells forming a hymeniform or subhymeniform layer; spores mostly medium sized to large; lamellae not or indistinctly collariate; stipe rudimentary, later often oblique or eccentric, with insititious or subinsititious to mycelioid base (unless rudimentary), hyphae pseudoamyloid (at least in the stipe), or all inamyloid, with or without clamp connections; on dead wood and leaves.

Type species: *M. neosessilis* Sing.

*M. polycystis* Sing.; *M. paulensis* Sing.; *M. linderi* Sing.; *M. rufoaurantiacus* Petch; *M. cecropiae* Dennis; *M. griseoroseus* (Mont.) Dennis; *M. ustilago* Sing.; *M. neosessilis* Sing.; *M. sessiliaffinis* Sing.; *M. sessilis* (Pat.) Sacc. & Syd.; *M. tenuissimus* (Jungh.) Sing.; *M. spaniophyllus* Berk., with var. *iguazuensis* (Sing. in Sing. & Digilio) Sing.; *M. sejunctus* Sing.; *M. pleurotelloides* Sing.

Cyphelloid species without hymenophore: *M. cyphella* Dennis & Reid. Possibly here also *Femsjonia natalensis* Cooke (acc. to Reid).

Sect. 11. *ALLIACEI* Kühner (1933, as Alliaceae). Pileus pigmented or not, with all epicuticular cells smooth, or with some finger-like appendices, at any rate not in form of broom cells; spores small to medium sized, rarely large (long); stipe central, with distinct basal mycelium, mostly with pruinate to velutinous covering but also often glabrous; hyphae inamyloid or very slightly pseudoamyloid; on dead wood and leaves, fronds, roots, or humus.

Type species: *M. alliaceus* (Jacq. ex Fr.) Fr.

*M. perlongispermus* Sing.; *M. copelandii* Peck; *M. smaragdinus* (Berk.) Sing.; *M. murrillianus* Sing.; *M. batistae* Sing.; *M. oligocystis* Sing.; *M. aimara* Sing.; *M. lolema* Beeli; *M. prasiosmus* (Fr.) Fr.; *M. olidus* Gilliam; *M. scorodonius* (Fr.) Fr.; *M. alliaceus* (Jacq. ex Fr.) Fr.; *M. ionides* Pat.; *M. latiuscolospermus* Sing.; *M. chordalis* Fr.; *M. pyrrhocephalus* Berk. (*M. elongatipes* Peck); *M. hinnuleiformis* Murr.; *M. epidryas* Kühn.; *M. zenkeri* Henn. (typus, non sensu Zenker, Fl. kam. nec Sing. 1964 nec Pegler); apparently also *M. subalpinus* Sing.; *M. platycystis* Sing.; *Gymnopus subagricola* Murr. (the last three with poorly developed epicutal hymenium, and not recently restudied), and *M. pegleri* Courtecuisse.

Species with only vacuolar pigments and stipe-hyphae partly slightly pseudoamyloid, often without clamp connections, should be separated in subsect. *Hydropodoides* Sing. (1982). Typical for this group are *M. marasmoides* (Sing.) Sing. and two undescribed species. But some of the species enumerated above would have to be inserted here also.

Sect. 12. *GLOBULARES* Kühn. (1933) (*Sympodia* Heim 1948). Epicutis and basal mycelium as well as habit (collybioid) of the preceding section, but with distinctly pseudoamyloid trama; pileus without typical setae.

Type species: *M. wynnei* Berk. & Br.

*M. violaceus* Henn.; *M. becolacongoli* Beeli; *M. superbus* Henn.; *M. staudtii* Henn.; *M. flavus* Sing.; *M. brunneolus* (Beeli) Sing.; *M. mesosporus* sing.; *M. viegasii* Sing. in Viegas; *M. pampicola* (Speg.) Sing. (Collybia, Speg.); *M. plumieri* (Lév.) Sing. (*Heliomycetes*, Lév.); *M. collinus* (Scop. ex Fr.) Sing. (Collybia, Quél.); *M. fissipes* (R. Maire) Sing. (Collybia, Mre.); *M. lilacinus* (Coker) Sing. (Collybia, Coker); *M. todeae* Bres.; *M. nigrodiscus* (Peck) Halling (*M. tenuifolius* (Murr.) Sing., *Gymnopus*, Murr; *G. glatfelteri* Murr.); *M. wynnei* Berk. & Br. (*M. globularis* Fr. in Quél.); *M. carpathicus* Kalchbr.; *M. tortipes* Berk. & Curt.; *M. oreades* (Bolt. ex Fr.) Fr. [*M. caryophylleus* (Schaeff. ex) Schröt.]; *M. ryssophyllus* Mont. in Berk. (ss. Pat.; *Dictyoploca*, Baker & Dale); *M. ditopotrama* Sing.; *M. poromycenoides* Sing.; *M. albogriseus* (Peck) Sing. (Collybia, Peck; Collybia *fimicola* Earle); *M. pseudocollinus* (Sing. in Sing. & Digilio) Sing.; *M. cohortalis* Berk. [with var. *hymeniicephalus* (Speg.) Sing., var. *arenicolor* Sing.]; *M. alachuanus* Murr. (*M. ludovicianus* (Murr.) Sing. non J.E. Planch.; *Gymnopus*, Murr.); *M. cibarius* Sing.; *M. myocephalus* Sing.; *M. niveus* Mont. (Collybia, Dennis; *Mycena marasmius* Murr.?); *M. riparius* Sing. in Sing. & Digilio; *M. silvicola* Sing. in Sing. & Digilio; *M. heliomycetes* Murr.; *M. arborescens* (Henn.) Beeli (Collybia, Henn.); *M. torquescens* Quél.; *M. cystidiosus* (A.H. Smith) Gilliam; *M. albertianus* Sing.; *M. goossensiae* Beeli; *M. witteanus* Sing.; *M. strictipes* (Peck) Sing.; obviously also *M. jodocodus* Henn., *M. polypus* (Kalchbr.) Reid, and *M. brunneodiscus* Pegler (= ? *M. subplancus* Henn.).

#### Reduced series: 81. **RIMBACHIA** Pat.

*Bull. Soc. Myc. Fr.* 7: 159. 1891.

Type species: *R. paradoxa* Pat.

Characters: Habit of *Arrhenia* i.e. spatuloid with a rather long (carpophores ± 4-8 mm high) pseudostipe and cup-shaped pileus, nutant so that the concave hymenial surface points downwards, very thin, not tough, with smooth hymenial surface or with a few low, obtuse, radial veins, base of the pseudostipe often disc-like or insititious; hyphae filamentous, inamyloid, but in the stipe slightly pseudoamyloid, with clamp connections; no gelatinous zones observed; basidia normal; cystidia none; spores >10 µm long and relatively narrow, cylindric, sometimes somewhat sausage shaped, inamyloid, smooth, hyaline; epicutis - weak or distinct *Rameales*-structure, not hymeniform, not gelatinized; pigment in young carpophores none, later dull colored in parts. Monomitic. On rotting fragments of mosses, palms, etc. Tropical.

*Development of the carpophores:* Much like *Arrhenia*, but unknown in detail.

*Area:* Neotropics.

*Limits:* The habit of the carpophores is different from both *Cymatella* and *Calyptella* from which *Rimbachia* differs also in the tendency to have some pseudoamyloid elements in the stipe trama, the only and perhaps doubtfully valid reason why *Rimbachia* is here inserted in the Marasmieae rather than close to *Cymatella*. *Rimbachia* differs from *Skepperiella* and *Cyphella* in the spore size, the habitat, and presence of pseudoamyloid hyphae. It differs strongly from *Rhodoarrhenia* in the non-gelatinized trama, the much less developed veins which are never meruliod, and the much larger spores. Corner's (1966) redescription of *Rimbachia paradoxa* is misleading since it is not based on a comparison with the type and differs from the latter as well as from *R. palmigena* in the meruliod hymenophore, the gelatinized (subgelatinous) walls, the small spores \*, and the habitat (lignicolous). It appears probable that Corner's interpretation of *Rimbachia paradoxa* was influenced by Lloyd who considered this species as a synonym of "*Rimbachia*" *pezizoidea* (*recte Rhodoarrhenia pezizoidea*), whereas Patouillard puts the two species in different genera (FH). *R. paradoxa* sensu Corner is probably a *Rhodoarrhenia*.

Redhead extends (*Can. Journ. Bot.* 62: 865-892. 1984) the circumscription of *Rimbachia* to such a degree that it includes also *Mniopetalum* (without a long, nutant pseudostipe, with different spores) and *Pleuromycenula* (with lateral stipe, inflated hyphae, and different spores), but he believes that *Rimbachia palmigena* is not congeneric but "should be sought for" in *Calyptella* (although it has a lateral stipe and much larger pilei - up to 11 mm and not cypelloid or solenoid - than in the Calyptellas known to me). Redhead includes also *Cantharellus furfuraceus* Petch in *Rimbachia*, but in spite of the extensive description given by Corner (1966) this species is still incompletely known with regard to some data and may belong in *Pleuromycenula*.

Under the circumstances, I believe that it is dangerous to attempt a broader generic concept of *Rimbachia* and that the habitat cannot at the same time serve as generically important character (as between *R. paradoxa* and *R. palmigena*) and be variable in the generic description.\*\* Since the pseudoamyloidity of the stipe hyphae remains the only truly distinguishing character between the type species and *R. palmigena*, it may rather be assumed that *Rimbachia*, like *Marasmius* sect. *Androsacei* is variable in this regard, but that the final position of *Rimbachia* in Collybieae

\* It is not so improbable (as implied by Corner 1966) that the spores are as long as indicated in my type studies of *R. paradoxa* (1945) since the relation between basidial length and spore length is about equal to that indicated by Corner himself for *Hymenogloea papyracea* (p. 229). Redhead (1984) finds the spores 9-12 × 4.8-6 µm.

\*\*Redhead says that "all Rimbachias are associated with bryophytes". On the type I have seen at least some carpophores rising from dead mosses; *Mniopetalum bisporum* grew on Bryophyta, living angiosperm leaves and branchlets, and on Pteridophyta at the type locality. *Cantharellus furfuraceus* grows according to Corner (1966) on "gravelly banks by roads, on mossy earth or on bare heaped earth". All these are Rimbachias sensu lato (Redhead).

or Marasmieae cannot be with certainty established at the present time. All Calyp-tellas in my notes are described as having inamyloid hyphae.

*State of knowledge:* The somewhat scanty material of the type species has been revised by Singer (1945); the second species is well known in its essential characters.

*Practical importance:* Unknown.

## SPECIES

*R. paradoxa* Pat.; *R. palmigena* Sing.

### Reduced series: 82. PHYSALACRIA Peck

*Bull. Torr. Bot. Cl.* 1: 2. 1882.

*Type species:* *P. inflata* (Schwein.) Peck.

*Syn.:* *Eoagaricus* Krieger, *Md. Acad. Sc. Bull.* 3: 8. 1923.

*Baumannella* Henn., *Engler's Bot. Jahrb.* 22: 543. 1895.

*Hormomitaria* Corner, *Monogr. Clavar.* p. 696. 1950.

*Characters:* Habit of the carpophores specific, "physalacrioid", i.e. the pileus mostly deformed to a globose or irregularly inflated, hollow club which is terminal on a short, thin, pseudostipe, the latter generally not subject to negative geotropism, and typically insititious, more rarely pileus vertically elongated and somewhat clavate; hymenial surface smooth, often in irregular fragments and concentrated in areas directed towards the ground and obliquely vertically exposed; stipe surface sterile, sometimes with *Rameales*-structure, and mostly with "oleocystidia" as are the sterile portions of the head; hyphae of the thin monomitic trama of the head filamentous, interwoven or running in strands of parallel hyphae, with clamp connections, inamyloid, usually thin-walled and often loosely arranged, not or slightly gelatinized; those of the stipe parallel with each other, also inamyloid, not gelatinized. Basidia normal, basidioles fusoid, some ampullaceous; sterigmata 2 or 4; cystidia and/or oleocystidia (mostly the latter) present, often with sterigmatoid apical outgrowth(s) or transitions to broom cells; cystidioles also often present; spores small to very large, ellipsoid, fusoid, oblong, or acicular, smooth, thinwalled, inamyloid, acyanophilic. On dead and living leaves and wood. - The spores may tend to become slightly brownish in overaged condition; the hyphal walls may become rather thick in the stipe.

*Development of the carpophores:* Gymnocalypous (see McGuire, *Mycologia* 31: 436. 1939, and Baker, *Bull. Torr. Bot. Cl.* 68: 266-270, figs. 1-23. 1941, also Corner 1950); stipitocalypous (Reijnders).

**Area:** Tropical and temperate America; tropical and Eastern Asia, Madagascar and tropical West Africa, Australia and New Zealand. One species was discovered by Reijnders in Europe (but probably not native), another was indicated by Heim in Spain but this latter is a species of Clavariaceae [*Clavicorona tuba* (Heim) Corner].

**Limits:** No difficulties are foreseen in the delimitation of this genus.

**State of knowledge:** The genus was studied by G.A. Baker and by Corner (1941 and 1950 respectively), and eleven species have been studied by the present author (*Flora Neotrop.* 17: 304-311. 1976).

**Practical importance:** Unknown.

## SPECIES

Sect. 1. **HORMOMITARIA** (Corner) Sing. (1976). Pileus vertically elongated, long-obclavate.

**Type species:** *Hormomitaria sulphurea* Corner

*H. sulphurea* (Corner) Sing.; possibly also *H. albidula* Corner (but without oleocystidia).

Sect. 2. **PHYSALACRIA**. Pileus subisodiametric, short-cylindric-conical, or ovate, mostly hollow.

**Type species:** *P. inflata* (Schwein.) Peck.

*P. clusiae* Sydow; *P. tenera* Sydow (*P. cryptomeriae* Reijnders); *P. andina* (Pat. & Lagerh.) Pat.; *P. concinna* Sydow sensu Corner vix Sydow; *P. aggregata* Martin & Baker; *P. orinocensis* Pat. & Gaill.; *P. sanctae-marthae* Martin & Baker; *P. langloisii* Ellis & Ev.; *P. inflata* (Schwein.) Peck; *P. brasiliensis* (Rick) Corner.

## Reduced series: 83. **DEIGLORIA** Agarer

*Mycotaxon*: 12: 188. 1980.

**Type species:** *D. pulchella* Agerer.

**Syn.:** ?*Eomycenella* Atk., *Bot. Gaz.* 34: 37. 1902.

**Characters:** Carpophores cyphelloid or pleurotoid-astipitate, with or without a pseudostipe; oleocystidia present in the hymenium and/or the sterile surfaces, the latter densely beset with dermatocystidia and often at least partly hymeniformly corticated; metuloids on sterile surface and more rarely on fertile hymenium present and these sometimes with amyloid wall; cystidia often with mucro or one to several finger-like appendages (approaching the Rotalis- or Siccus-type of broom cells), or

else capitate or subcapitate (and then much like those of *Gloiocephala*); hymenophore varying from absent to veined-sublamellar (but then without differentiated cheilocystidia); basidioles mostly ± fusoid or subampullaceous; basidia 4-spored; spores oblong to fusoid, more rarely ellipsoid, with thin smooth, inamyloid wall, hyaline, sometimes somewhat browning when overaged (or from the exudatea); hyphae not gelatinized, with clamp connections, inamyloid. Basal mycelium or rhizomorphs sometimes present. On wood as well as herbaceous matter (including Pteridophyta).

*Development of the carpophores:* Unknown.

*Area:* Tropical South America (Paraguay to Colombia) and Hawaii.

*Limits:* As long as only three species were known, I combined the two closer to *Gloiocephala* with the latter as section *Sessiles* Sing. (*Fl. Neotr.* 17: 302. 1976) and the one closer to *Physalacria* with *Physalacria* as sect. *Subpeltatae* Sing. l.c. p. 311). Four years later, Agerer published his new genus *Deigloria* which is obviously very close to both my sections, especially the former. Since structure and many other characteristics appear to be intermediate or transient between *Gloiocephala* and *Physalacria* but the habit of the carpophores markedly different from both, it seems best at present to combine both *Sessiles* and *Subpeltatae* under Agarer's generic name. The constant presence of oleocystidia or oleodermatocystidia combined with the frequent development of broom cells make it now quite clear that *Physalacriaceae* is a synonym of Tricholomataceae, and particularly close to Marasmieae (*Marasmius paulensis* has similar oleocystidia and also broom cells!). The question arises rather how to delimit *Deigloria* from *Marasmius* sect. *Neosessiles*. Aside from the constant development of well formed lamellae in the species of *Neosessiles*, these are also characterized by the composition of the hymeniform epicutis which consists exclusively or almost exclusively of broom cells. Furthermore all except one (*M. griseoroseus*) species of *Marasmius* have a true, lateral to eccentric (to central) stipe.

*State of knowledge:* I have complete notes on four species and the four original species of *Deigloria* must be added to these.

*Practical importance:* Unknown.

## SPECIES

*D. subpeltata* (Redhead) Sing. (*Physalacria subpeltata* Redhead, *Mycotaxon* 10: 46. 1979); *D. paraguayensis* (Speg.) Agerer; *D. sessilis* (Sing.) Sing. (*Gloiocephala sessilis* Sing., *Fl. Neotrop.* 17: 303. 1976); *D. anastomosans* Sing. (*Gloiocephala anastomosans* Sing., *Fl. Neotrop.* 17: 303. 1976); obviously also *D. pulchella* Agerer, and according to Agerer also *D. amoena* Agerer, *D. modesta* Agerer, and *D. pulcherrima* Agerer.

Grevillea 21: 34. 1892.

Type species: *G. epiphylla* Mass.

Syn.: ?*Discocyphella* Henn., Warburg's Monsunia 1: 43. 1900.

**Characters:** Stipitate, rarely sessile, sometimes, spatuloid, the hymenial surface directed downwards, hymenophore present or absent, if present - vein-like, sometimes meruliod, or lamellate; pigment in pileus and stipe present or absent, in the latter often abundant; epicutis of the pileus consisting of a hymeniform layer of vesiculose to somewhat elongated but generally short, obtuse cells sometimes swelling in alkali, rarely beset with short outgrowths, dermatocystidia of the pileus long and striking, often metuloid, and/or characteristically subcapitate or capitate or with a hyphous effilcate outgrowth, sometimes pseudoamyloid and cyanophilic, but not of the type represented by the *Crinipellis*-hairs; basidia normal, but often not formed in culture; basidioles fusoid; hymenial cystidia present or absent, if present usually capitate or subcapitate, more numerous towards the margin of the pileus; spores medium sized to very large, ellipsoid to fusoid-cylindric, clavate or oblong, smooth, inamyloid; hyphae of the monomitic trama inamyloid or weakly to strongly pseudoamyloid, with clamp connections. On leaves, culms, wood, etc., both living and dead (Pteridophyta, Coniferae, Mono- and Dictyledones), attached by an insititious base or by basal mycelium, sometimes accompanied by dark rhizomorphs.

**Development of the carpophores:** Very young carpophores show an exposed inferior hymenial zone, but smaller primordia have not been studied.

**Area:** Most species tropical, few occurring in the temperate zones.

**Limits:** This genus is closely related to *Marasmius* sect. *Epiphylli* and sect. *Alliacei*; it differs however, from the former in the presence of very characteristic dermatocystidia and the hymenial cystidia which are either absent in *Gloiocephala* or of a different type (not fusoid-ampullaceous); furthermore there is a tendency in *Gloiocephala* to have a basal mycelium (which is absent in *Marasmius* sect. *Epiphylli*) and/or strongly pigmented pileus and stipe (the *Epiphylli* are practically pigmentless in the pileus). The non-insititious species of *Gloiocephala* differ from all those *Marasmius*-species which are equally non-insititious by the absence of a hymenophore or by much smaller size and different habit (not collybioid), or both. The centrally stipitate non-insititious species of *Gloiocephala* have a pileus always smaller than 5 mm in diameter. *Gloiocephala*, as far as pigmented, insititious, lamellate forms are concerned differs from *Marasmius* sect. *Leveilleani* by smooth epicuticular elements and the presence of capitate cystidia.

The genus *Discocyphella* has been described in such a manner as to suggest that it is characterized by a gelatinized trama, and Patouillard, on the basis of the description, believed it to be congeneric with *Cymatella* and created a section of the latter to accommodate the Discocyphellas. However, no such gelatinized Cymatellas

have ever been collected. The type species of Hennings' genus has been lost. A second species, not the type, was described by Hennings and is preserved (B). This species, *D. ciliata* Henn., is a good and typical *Gloiocephala*. Its trama is not gelatinous.

Some species with smooth hymenial surface which do not show the characters of *Gloiocephala* agree in all characters with the section *Epiphylli*. These species, accordingly, have been left in *Marasmius* (*M. martini* Sing., *M. sanctixaverii* Sing.).

With all these data at hand, I cannot agree with those mycologists who on the basis of their knowledge of the few temperate representatives of this genus and *Marasmius* sect. *Epiphylli* tend to minimize the differences between these taxa; it is perhaps possible to state that all characters of *Gloiocephala*, unless considered in character-correlations, also occur in *Marasmius*.

*State of knowledge:* 25 species are now well known and enumerated below. See Pl. 65; 66.

*Practical importance:* Some species may be pathogenic on crop- or garden plants.

## SPECIES

Sect. 1. *GLOIOCEPHALA*. Pileus and stipe covered with dermatocystidia or hairs not longer than 108 µm, often much shorter.

*Type species:* *G. epiphylla* Mass.

Subsection *Macrosporae* Sing. (1974). Spores 11-23 × 3.3-7.5 µm; on Monocotyledones.

*Type species:* *M. inobasis* Sing.

*G. inobasis* Sing.; *G. longisperma* Sing.; *G. palmarum* Sing.; *G. menieri* (Boud.) Sing.; *G. caricis* (Karst.) Bas; obviously also *Marasmius menieri* Boudier sensu Corner non Boud. (*Gloiocephala* sp. Bas, *Persoonia* 2: 86. 1961) and *G. culmicola* Sing. ined.

Subsection *Religiosae* Sing. (1974). Spores not longer than 12.8 µm, mostly smaller; pileus pigmented or not (if not pigmented: on conifers).

*Type species:* *G. religiosa* Sing.

*G. religiosa* Sing.; *G. ciliata* (Henn.) Sing. (*Discocyphella*, Henn.); *G. podocarporum* sing.; *G. radina* Sing.; *G. caucasica* (Sing.) Sing. (*Marasmius caucasicus* Sing.. Rev. Myc. 2: 230. 1937).

Subsection *Confusae* Sing. (1974). Spores as in the preceding subsection; pigment none (except for the resinous incrustations present in some species). On Dicotyledones exclusively.

*Type species:* *G. confusa* Sing.

*G. confusa* Sing.; *G. alvaradoi* Sing.; *G. mycenoides* Sing.; *G. spathularia* Sing.; *G. epiphylla* Mass.; *G. quitensis* Sing. and obviously also *M. epifagus* Gilliam.

Sect. 2. *LONGIFIMBRATI* Sing. (1974). Pileus covered with setoid hairs up to 450 µm long.

Type species: *G. longifimbriata* sing.

*G. occidentalis* Sing.; *G. capillata* Sing.; *G. longicrinita* Sing.; *G. longifimbriata* Sing. (with several varieties); *G. lamellosa* Sing.; *G. cinnamomea* Sing.; *G. allomorpha* Sing.; obviously also *G. albocapitata* (Petch) Sing.

Sect. 3. *SPATHULARIAE* Sing. (1976). Carpophores spathuloid or cochleate; hymenophore mostly venose; spores minute, up to 6 µm long.

Type species: *G. spathularia* Sing.

*G. spathularia* Sing.; *G. lutea* Sing.

#### Reduced series: 85. **PALAEOCEPHALA** Sing.

*Sydowia* 15: 60. 1961.

Type species: *Palaeocephala cymatelloides* (Dennis & Reid) Sing.

Characters: Those of *Gloiocephala*, but without hymenial cystidia, without dermatocystidia and hairs, without pigment in the type species, without hymenophore in the type species, with abundant basal mycelium, hyphae pseudoamyloid. Small carpophores on leaves, causing leaf spots.

Development of the carpophores: Unknown.

Area: Africa (Sierra Leone).

Limits: This genus is close to the sect. *Globulares* or *Alliacei* of *Marasmius* but differs in much smaller size, complete lack of a hymenophore, thin trama of the pileus. It is, among the reduced genera, closest to *Gloiocephala* from which it differs in the characters enumerated in the generic description given above.

State of knowledge: A single species is known until now.

Practical importance: Unknown.

#### SPECIES

*P. cymatelloides* (Dennis & Reid) Sing. (*Marasmius*, Dennis & Reid).

*Sydowia* 14: 279. 1960.

*Type species:* *M. bifida* Sing.

*Characters:* Habit marasmoid-stereoid, stipe simple or branched, insititious; carpophores very small, rising from black rhizomorphs, without a hymenophore or with few vein-like elevations on the fertile underside of the pileus; epicutis hymeniform or subhymeniform, consisting of cells reminiscent of the broom cells of the *Rotalis*-type in *Marasmius*; spores smooth, hyaline, ellipsoid, medium sized, inamyloid; cystidia and dermatocystidia none; hyphae with clamp connections, inamyloid. On woody litter (Pl. 67, 9).

*Development of the carpophores:* Unknown.

*Area:* Part of tropical America.

*Limits:* This genus is not fully analogous with *Marasmius*, section *Hygrometrici* although it approaches it as much as *Gliocephala* approaches the sect. *Epiphylli* or *Hymenogloea* the sect. *Alliacei*. It differs from the *Hygrometrici* in the smooth or venulose-smooth hymenium and the tendency of the stipes to branch, in the rhizomorphs (which are black and beset with lacerated setae in the type species). The epicuticular elements although reminiscent of the broom cells of the *Rotalis*-type as often seen in the *Hygrometrici*, are characterized by their tendency to bear, aside from individual setulae, dense crust-like aggregations of setulae on their upper surface, a tendency not observed in the *Marasmii* studied by us.

*State of knowledge:* Thus far, a single species is known. However, in view of the extremely small size of the carpophores, it is likely that similar fungi are not so rare as might be assumed but that they have been overlooked. The type species is completely known.

*Practical importance:* Probably none.

## SPECIES

*M. bifida* Sing.

*Sydowia* 14: 279. 1960.

*Type species:* *E. phalaropus* Sing.

*Characters:* Habit marasmoid-helotiod, stipe simple, with scanty basal mycelium; carpophores small, not rising from rhizomorphs, without a hymenophore; epicutis hymeniform or subhymeniform, consisting of cells reminiscent of the broom cells of the *Rotalis*-type in *Marasmius*; spores smooth, hyaline, ellipsoid, medium sized,

inamyloid; cystidia and dermatocystidia none; hyphae with clamp connections, Pseudoamyloid. On litter (Pl. 67, 10).

*Development of the carpophores*: Unknown.

*Area*: Part of tropical America.

*Limits*: The genus is very close to both *Hymenogloea* and *Manuripia*, differing from the former in size, and in the character of the epicuticular elements (broom cells in the case of *Epicnaphus*), from the latter in pseudoamyloid hyphae and the basal mycelium. It is obviously closely related to *Marasmius* but cannot directly be linked with any known section of the latter since, in the non-insititious sections, the only ones with pseudoamyloid hyphae have another type (*Siccus*-type or smooth vesiculose elements) of epicuticular elements. It is therefore admitted as an autonomous genus.

*State of knowledge*: Thus far, a single species is known. However, it is likely that similar fungi may be found in the future. The type species is completely known.

*Practical importance*: Probably none.

## SPECIES

*M. phalaropus* Sing.

### Reduced series: 88. HYMENOGLOEA Pat.

*Ess. taxon.*, p. 146. 1900.

*Type species*: *H. riofrioi* Pat.

*Syn.*: *Libellus* Lloyd, *Myc. Writ.*, Lett. 45: 6. 1913.

*Characters*: Habit collybioid-stereoid, i.e. reminding one of the large tropical stipitate Stereums (*Cymatoderma*, etc.) and at the same time of a large species of *Marasmius* sect. *Alliacei* or *Sicci*, long-stipitate with a central stipe; hymenophore none; hymenial surface on the lower side of the thin pileus - smooth. All parts of the carpophore well pigmented; base of stipe with abundant tomentum and strigose from the basal mycelium; dermatocystidia none; epicutis of pileus hymeniform, consisting of swollen smooth cells without interspersed setae; spores cylindric to fusoid, medium sized, inamyloid; hyphae pseudoamyloid. On leafmold in tropical forest (Pl. 67, 11).

*Development of the carpophores*: Unknown.

*Area*: Tropical America.

*Limits*: The genus is very striking in fresh as well as in dried condition. The very thin trama of the pileus and the completely smooth hymenial surface, also the bright pigment changing color on dehydration, and disappearing (bleaching) in alkali

mounts, are characters which separate *Hymenogloea* from the sect. *Globulares* of *Marasmius* which is otherwise roughly parallel, but never shows the slightest tendency towards smooth or even venose hymenial surfaces.

*Hymenogloea* forms by far the largest of all the carpophores known in the reduced series. Its pigments remind one rather of certain species of *Marasmius* sect. *Sicci* (e.gr. *M. ruber*) than of sect. *Globulares*, or of other reduced genera. The latter are, besides, separated from *Hymenogloea* by the characters emphasized in the key. For all these reasons, *Hymenogloea* seems to be a good, perfectly autonomous genus, easy to delimit and to recognize in nature, not at all related to *Craterellus*, *Stereum*, or *Troglia*.

*State of knowledge:* The only species is completely known.

*Practical importance:* Unknown.

## SPECIES

*H. papyracea* (Berk. & Curt.) Sing. (*Craterellus*, Berk. & Curt.; *Libellus*, Lloyd; *Stereum rufum* Pat.; *Hymenogloea*, Pat.).

### Subtribus *Crinipellinae* Sing.

*Flora Neotropica* 17: 8. 1976.

Long, consistently (at least in the larger middle portion) thick-walled and pseudoamyloid hairs or thick-walled, long, incrusted hairs present (not as part of a hymeniform epicutis, but often arising from a hypotrichium which functions as hypodermium), or else pseudoamyloid flagelliform appendages on the epicuticular hairs present. Hyphae inamyloid, generally with clamp connections; spores typically either inamyloid or pseudoamyloid, cyanophilic.

*Type genus:* *Crinipellis* Pat.

## 89. CRINIPELLIS Pat.

*Journ. Bot.* 3: 336. 1889; em. Earle, *Bull. N.Y. Bot. Gard.* 5: 414. 1909.

*Type species:* *C. stipitaria* (Fr.) Pat.

*Characters:* Habit of the carpophores collybioid or marasmoid, rarely slightly pleurotoid; pileus and usually also stipe covered with thick-walled elements which are usually distinctly hair-shaped (Pl. 63a-f), and pseudoamyloid to almost amyloid, smooth, well separated from the trama of pileus by a hypotrichial layer, hymenophore always well developed, lamellate; cheilocystidia present (Pl. 63, 2c, g); cystidia on the sides of the lamellae in one group of species frequent (Pl. 58, 2f), not pseudoamyloid, rarely metuloid and pseudoamyloid as in *Chaetocalathus* sect.

*Holocystis* and *Lachnella* sect. *Metuloidifera*; spore print white or nearly so; spores (Pl. 63, 3) hyaline, of various shapes, smooth, inamyloid, thin-walled but after prolonged presence on the carpophore after maturity (without germinating) often becoming somewhat thick-walled, and in one species even septate (i.e. finally bicellular), cyanophilic; basidia without siderophilous granulosity, 4-spored, more rarely some basidia in a specimen with less than 4 sterigmata, often more or less deformed (cystidioles) with all transitions to basidioles (Pl. 63, 2a); stipe central or eccentric, not reduced to a papilla, insititious, but sometimes rising from white, at times pilose, rhizomorphs; trama inamyloid; hyphae with clamp connections. On dead and living plants, especially Gramineae and various trees and shrubs, usually on stems, roots, bamboo sticks, dead or living branches, fruits, etc.

*Development of the carpophores:* Unknown.

*Area:* Cosmopolitan excepting the Antarctica, but many more species in the subtropics and tropics than in temperate regions.

*Limits:* At present all species with pseudoamyloid hairs on both pileus and stipe are considered *Crinipellis* if there is a functional stipe and a well developed hymenophore (lamellae). Similar but not pseudoamyloid hairs are observed on some species of *Marasmiellus* on the pileus, and others of that same genus on the stipe. Those species of *Marasmius* and related "cyphelloid" genera which have similar hairs can easily be distinguished by the presence of a hymeniform or at least broom-cell-bearing epicutis. Consequently, even if these elements are occasionally pseudoamyloid as in *M. chrysochaetes* such species are no longer considered to belong in *Crinipellis*. The hiatus between *Crinipellis* and the genera just mentioned is considerable, and no difficulties are discovered with regard to the delimitation of the genus.

*State of knowledge:* The genus has been monographed by the present author in 1942 and the diagnostic characters as well as the intrageneric classification were worked out then. In the following thirty year numerous new species have been discovered, particularly in the neotropics and in Africa. They are here incorporated. The total number of species known at present is: 63.

*Practical importance:* The most important pathogenic species in *Crinipellis perniciosa* which is responsible for the krulloten- or witch-broom disease of cocoa.

## SPECIES

Sect. 1. *CRINIPELLIS*. Pileus some shade of stramineous or brown, or pigmentless, frequently chestnut to ferruginous-brown in wet, and more dull stramineous-tan in faded condition; with KOH merely turning darker or not reacting; stipe if less than 7 mm long, strictly central and straight and not white, but more frequently the stipe is longer than 7 mm and then also usually central and more or less straight, more rarely inconstantly slightly eccentric and curved when mature, insititious; if stipe is eccentric, spores as in sect. *Eccentricae*, or different.

*Type species: C. stipitaria* (Fr.) Pat.

Subsection *Macrosphaerigerae* Sing. (1976). Spores more than 9  $\mu\text{m}$  broad, subglobose.

*Type and only known species: C. macrosphaerigera* Sing.

Subsection *Crinipellis* (Stipitarinae Sing. (1942)). Spores smaller or much more elongated than in the preceding subsection; cystidia absent on the sides of the lamellae or present only as cystidioles in old carpophores (or where that lamellae have been bruised in situ), or as cheilocystidia (scattered a short distance from the edge); if cystidioles are present, these are degenerated basidioles.

*Type species: C. stipitaria* (Fr.) Pat.

*C. carecomoeis* (Berk. & Curt.) Sing.; *C. gracilis* Sing.; *C. rustica* Sing.; *C. peckii* (Murr.) Sing.\* (?*C. calderi*, Pegler); *C. urbica* (Mont.) Dennis; *C. subtomentosa* (Peck) Sing.; *C. mauretanica* Maire; *C. megalospora* Sing. in Sing. & Digilio; *C. perpusilla* (Speg.) Sing. (*C. bambusae* Pat.); *C. bisulcata* (Pat. & Gaillard) Pat.; *C. pseudostipitaria* Sing.; *C. catamarcensis* Sing.; *C. schini* Sing.; *C. atrobrunnea* Pat.; *C. missionensis* Sing.; *C. ghanaensis* Sing. apud Pegler; *C. zonata* (Peck) Pat.; *C. herrerae* Sing.; *C. septotricha* Sing.; *C. stipitaria* (Fr.) Pat.; *C. molfinoana* (Speg.) Sing.; *C. podocarpi* Sing.; *C. stupparia* (Berk. & Curt.) Pat. (*C. sub-stipitaria* Stevenson); *C. coroicae* Sing.; *C. tenuipilosa* Sing. in Sing. & Digilio; *C. hirticeps* (Peck) Sing.; *C. maxima* A.H. Smith & Walter; *C. campanella* (Peck) Sing.; *C. setipes* (Peck) Sing.; *C. piceae* Sing.; *C. micropilus* (Reichardt) Sing.; *C. mexicana* Sing.; *C. patouillardii* Sing.; *C. foliicola* Sing.; *C. phyllophila* Sing.; *C. dipterocarpi* Sing.; *C. dicotyledonum* Sing. in Sing. & Digilio; probably also *C. omotricha* (Berk.) Reid.

Subsection *Heteromorphinae* Sing. (1942). Characters like those of the preceding subsection, but pleurocystidia differentiated.

*Type species: C. minutula* (Henn.) Pat.

*C. commixta* Sing. in Sing. & Digilio, with var. *junia* Sing.; *C. minutula* (Henn.) Pat.; *C. pseudosplachnoides* (Henn.) Pat. ex Sing.; *C. galeropsidoides* Sing. ined.

Sect. 2. *METULOIDOPHORAE* Sing.\*\* Metuloids present; spores similar to those of subsect. *Macrosphaerigerae*; pileus not greening or graying with KOH (5%).

*Type species: C. metuloidophora* Sing.\*\*\*

*C. metuloidophora* Sing.

Sect. 3. *EXCENTRICINAE* (Sing.) Sing. (1976). Stipe at first central but soon becoming eccentric, mostly relatively short and distinctly curved, 2-7 mm long;

\*c.n. (*Heliomycetes peckii* Murr., *N. Am. Fl.* 9: 248. 1915).

\*\*sect. nov. Hymenio metuloidophoro. Typus: *C. metuloidophora* Sing.

\*\*\*Praesentia metuloideorum ab aliis speciebus differt. Sporis (11)-14-15 × (7.5)-9.5-11.5  $\mu\text{m}$ . In Quercetis Columbiae, A.M. Cleef 6602 (NY), typus.

pileus and/or stipe tending to be white or whitish at first (excepting sometimes the very center of the pileus). The great majority of the spores smaller than or up to 10.5  $\mu\text{m}$  in length and half as broad as long or narrower. Cheilocystidia either ventricose below with long and relatively thin apical neck, or strongly apically branched setulose. (Pleuro-)cystidia at times present. Surface of the pileus not greening or graying with KOH (5%).

Type species: *C. excentrica* (Pat. & Gaillard) Pat.

*C. excentrica* (Pat. & Gaillard) Pat.; *C. myrti* Pat. apud Pat. & Lagerheim; *C. albipes* Sing.

Sect. 4. *GRISENTINAE* (Sing.) Sing. (1976). Pileus either colored as in sect. *Crinipellis*, or else bright pink to red, in the former case with pleurocystidia, in the latter case without or with scarce pleurocystidia, in both cases distinctly turning gray to green when treated with a drop of KOH or NaOH (5%) on the surface of the pileus and/or the hairs are greenish or green incrusted when seen under the microscope in KOH or NaOH mounts.

Type species: *C. mirabilis* Sing.

*C. alkalivirens* Sing.; *C. trichialis* (Lév.) Pat.; *C. sapindacearum* Sing.; *C. tucumanensis* Sing.; *C. corticalis* (Desm.) Sing.; *C. dusenii* (Henn.) Sing. apud Pegler; *C. rubida* Pat. & Heim; *C. austrorubida* Sing.; *C. mirabilis* Sing.

Sect. 5. *IOPODINAE* (Sing.) Sing. (1976). Pileus bright colored, red, carmin-purple, crimson, lilac, violet, not greening or graying with KOH or NaOH.

Type species: *C. iopus* Sing.

Subsection *Iopodinae* (Sing.) Sing. (1976). Pileus centrally stipitate and stipe mostly straight, insititious, elongated and more than three times as long as the diameter of the pileus. Spores either long-fusoid to oblong and not broader than 4.7  $\mu\text{m}$ , or else ellipsoid and then not more than 4  $\mu\text{m}$  broad, Q = 2 or larger.

Type species: *C. iopus* Sing.

*C. iopus* Sing.; *C. purpurea* Sing.; *C. hygrocybooides* (Henn.) Sing.; *C. rubiginosa* Pat. (if different from the preceding species).

Subsection *Insignes* Sing. (1974). Pileus bright colored; stipe shorter than three times the diameter of the pileus, mostly curved or eccentric, insititious or with fibrillose-myceloid base; spores as in the preceding subsection or broader. Often parasitic.

Type species: *C. insignis* Sing.

*C. insignis* Sing.; *C. eggersii* Pat. apud Pat. & Lagerheim with var. *flavipes* Sing.; *C. palmarum* Sing. apud Pegler; *C. sublivida* Murr.; *C. siparunae* Sing.; *C. trinitatis* Dennis; *C. perniciosa* (Stahel) Sing. (Marasmius, Stahel).

*Lilloa* 8: 518. 1942.

*Type species:* *C. craterellus* (Dur. & Lév.) Sing.

**Characters:** Habit pleurotoid; pileus pilose with thick-walled, smooth pseudoamyloid to almost amyloid hairs which are very long and distinctly separated from the trama of the pileus by a hypotrichial layer; hymenophore well developed, lamellate; spores hyaline, thin-walled, eventually sometimes becoming somewhat thick-walled, smooth, inamyloid or pseudoamyloid, cyanophilic; basidia without carminophilous granulosity, 4-spored, or more rarely with an inconstant, lower number of sterigmata; cheilocystidia always present, cystidia on the sides of the lamellae also often present and either entire (then strongly incrusted by a crystalline incrustation) or variously forked or divided, very frequently pseudoamyloid; stipe rudimentary or more rarely absent, never directly attached to the substratum (since it has lost its function - the pileus itself being attached to the substratum); trama nonamyloid; hyphae with numerous clamp connections. On wood, bamboo, leaves, bark, sticks, and stems, etc.

**Development of the carpophores:** J. de Seynes has given some data on the development of *C. craterellus* (*Ann. Soc. Linn. Maine et Loire* 11: 1-10. 1869); in *C. paradoxus*, the youngest buttons (0.2 mm diam.) are woolly balls with an apical umbo which becomes the rudimentary stipe when the outside portion (margin of the pileus) grows strongly and the stipe remains almost unchanged. The woolly connection between pileus-margin and stipe breaks, and the hymenium becomes visible but some rest of the woolly covering may remain on the stipe and the rim of the margin which is strongly fimbriate. The development of the carpophores in this genus is important for the interpretation of the stipe, stipe rudiment and pseudostipe. The protuberance situated at the side of the hymenophore is here interpreted as rudiment of a stipe and the stalk-like organ at the side of the surface of the pileus is called pseudostipe since the pileus is formed first.

**Area:** Almost cosmopolitan but predominantly tropical and Atlantic, absent from large areas of the temperate zones.

**Limits:** Species with the stipe reduced to a button which is not attached to the substratum, are not found in *Crinipellis*, and a combination of pleurotoid habit and either pseudoamyloid cystidia or pseudoamyloid spores is also not found in that genus. These characters determine *Chaetocalathus* as natural genus, clearly different from *Crinipellis*. The presence of a hymenophore distinguishes *Chaetocalathus* from the reduced forms such as *Lachnella*.

**State of knowledge:** The species of this genus are well known. They have been monographed by the author, together with *Crinipellis*, in *Lilloa* 8: 441-534. 1942; *Flora Neotropica* 17: 53-57. 1976. 15 species are admitted. See Pl. 63, 3h, i; 63, 4.

**Practical importance:** None, as far as known at present.

## SPECIES

Sect. 1. *CHAETOCALATHUS* (*Oligocystis* Sing. 1942). Pseudoamyloid seta-like, or metuloid bodies in the lamellae absent; only inamyloid cystidia and/or cheilocystidia present; spores often pseudoamyloid.

Type species: *C. craterellus* (Dur. & Lév.) Sing.

*C. craterellus* (Dur. & Lév.) Sing. (*Pleurotellus patelloides* Orton); *C. fragilis* (Pat.) Sing.; perhaps also *Pleurotus eremita* Maire.

Sect. 2. *MERISTOCYSTIS* Sing. (1942). Pseudoamyloid setoid bodies present on the lamellae; these bodies relatively thin, acute, mostly branched. Eastern hemisphere and pantropical species.

Type species: *C. africanus* (Pat.) Sing.

*C. pachytrichus* Sing.; *C. bicolor* (Pat. & Demange) Sing.; *C. congoanus* (Pat.) Sing.; *C. africanus* (Pat.) Sing.; *C. paradoxus* (Henn.) Sing.; *C. columellifer* (Berk.) Sing.; *C. hispidus* (Mass.) Sing.

Sect. 3. *HOLOCYSTIS* Sing. (1942). Cystidia with thick pseudoamyloid walls, metuloid, entire or with up to four apical appendages, cristate, or occasionally with one effiliate appendage, generally incrusted by crystals, 4-12.5 µm in some species up to 32 µm broad, not setiform. Neotropical and pantropical.

Type species: *C. carneliacuber* Sing.

*C. niduliformis* (Murr.) Sing.; *C. liliputianus* (Mont.) Sing. (*Marasmius nidulus* Berk. & Curt.; *Crinipellis calosporus* Pat.); *C. galeatus* (Berk. & Curt.) Sing.; *C. asperifolius* (Pat.) Sing.; *C. carneliacuber* Sing.; *C. aurantiacus* Sing.

## 91. AMYLOFLAGELLULA Sing.

*Darwiniana* 14: 14. 1966.

Type species: *Cyphella pulchra* Berk. & Br.

Characters: Carpophores stipitate or not solitary or densely crowded, often arising from white rhizomorphs; the terminal articles of the hypotrichium with flagelliform, very thin, strongly pseudoamyloid appendages; otherwise much like *Crinipellis* and *Chaetocalathus*; but hymenophore present or absent; stipe if present stipe if present generally short and curved.

Development of the carpophores: Unknown in detail; the hymenophore is sometimes late in forming, often absent in small carpophores and present in larger ones.

Area: Tropical America, Africa, and Asia.

Limits: The characteristic structure of the epicuticular elements makes the delimitation of the genus easy.

*State of knowledge:* Until now four species are known two of these have been studied by this author.

*Practical importance:* *A. pulchra* causes "white stem blight" or "thread blight" on *Thea* and *Castanopsis* (Dennis 1957, Kobayashi 1971).

## SPECIES

*A. pulchra* (Berk. & Br.) Sing. (*Cyphella*, Berk. & Br.); *A. pseudoarachnoidea* (Dennis) Sing. (*Marasmius*, Dennis); obviously also *A. inflata* Agerer & Boidin and *A. verrucosa* Agerer & Boidin; probably also *Cyphella byssacea* Henn. & Nym.

### Reduced series: 92. LACHNELLA Fr.

*Corp. Flor. Proc. I. Floram Scanicam*, p. 343. 1836.

*Type species:* *Peziza alboviolascens* A. & S. ex Fr.

*Syn.:* *Cyphelloclathus* Agerer, *Mycologia* 73: 491. 1981.

*Characters:* Same as in *Chaetocalathus*, but hymenophore absent, habit more distinctly cyphelloid, generally smaller, gregarious.

*Development of the carpophores:* The smooth hymenial surface of dried material is in the primordial and young stage of the carpophores covered by recurved hairs, later opening by expansion of the margin.

*Limits:* The limits of this genus against the other marasmioid genera do not present any difficulties. It is obvious that *Lachnella* is closest to *Chaetocalathus* which differs in the well developed hymenophore.

*State of knowledge:* At present, we know only five species which the author has studied personally.

*Practical importance:* Hardly any.

## SPECIES

Sect. 1. *LACHNELLA*. Pseudoamyloid hairs more or less echinulate (by crystals); cystidia none; spores and basidia large.

*Type species:* Same as in genus.

*L. alboviolascens* (A. & S. ex Pers.) Fr. (*Cyphella*, Crouan); *L. villosa* (Pers. ex Schw.) Gillet. (*Peziza*, Pers. ex Schw.; *Cyphella*, Crouan); *L. tiliae* (Peck) Donk apud Sing. (*Peziza*, Peck; *Cyphella*, Cooke).

Sect. 2. *AUSTRALES* Sing. ad int. Pseudoamyloid hairs more sparsely or scarcely crystalliferous; spores and basidia smaller. This is undoubtedly a transition towards the Flagelloscyphae. The typical species is *L. australis* Sing. (from the south-

temperate regions); apparently also here: *Flagelloscypha subnuda* Agerer; *L. paraguayensis* W.B. Cooke and *Nochascypha stricta* Agerer; probably also *Solenia idahoensis* (Rectipilus, Agarer) and *Calathella davidi* Reid (Rectipilus, Agerer).

Sect. 3. **METULOIDIFERA** Sing. (1961). Pseudoamyloid elements smooth or little incrusted; gigantic hymenial metuloids with thick crystalline incrustation and pseudoamyloid walls present.

Type and only species: *L. cecropiae* Sing.

Reduced series: 93. **FLAGELLOSCYPHA** Donk apud Sing.

*Lilloa* 22: 312. 1951 em.

Type species: *Cyphella minutissima* Burt.

Syn.: *Calathella* Reid, *Persoonia* 3: 122. 1964.

*Cephaloscypha* Agerer, *Sydworia* 27: 193. 1975.

*Nochascypha* Agerer, *Mitt. Bot. München* 19: 262. 1983.

**Characters:** Carpophores cyphelloid, i.e. astipitate, cup-shaped or tubular-turbinate, or narrowly infundibuliform, thinly membranous, entirely villous on the outer sterile side, with smooth hymenial surface, small, gregarious, more rarely solitary; trama monomitic, consisting of not gelatinized, clamp-bearing, inamyloid hyphae; spores hyaline, smooth, with homogenous wall, acyanophilic inamyloid, of variable shape, subglobose, ellipsoid, ovoid, amygdaliform, cylindric, or fusoid-cylindric and somewhat falcate, medium sized, not over 12.5  $\mu\text{m}$  long, and generally not so broad as in *Lachnella*; basidia normal; basidioles fusoid, subampullaceous or narrowly clavate; cystidia and pseudocystidia and meruloids absent but cystidioles in the zone of the rim of the cups often forming transitions between hairs and basidioles, these cystidioles if present inconspicuous or irregular-crooked, otherwise like 1-sterigmatic basidic remaining non-sporulating; surface hairs forming the villous covering either thickwalled and then sometimes swelling and spirally distorted in KOH (5%) (but the apex often thin-walled, or thin- to moderately thick-walled with "flagelliform"-extended apex, the latter often not incrusted but otherwise generally incrusted by fine crystals of calcium oxalate (insoluble in acetic acid, somewhat soluble in KOH, soluble in HCl and HNO<sub>3</sub>) inamyloid or very weakly pseudoamyloid (visible only in superposition of several hairs and perhaps restricted to an inner wall layer, reaction "disappearing" in old herbarium material), generally aseptate, but eventually often with secondary septa especially at the apex, or else remaining aseptate, very long and thin, rarely with swollen, subcapitate apex, hyaline, often rising from a multiseptate hyphal hypotrichium. On all kinds of vegetable débris, leaves, wood, herbaceous stems, ferns, etc.

**Development of the carpophores:** Young dried carpophores are a globose mass of hairs enveloping the immature hymenium; detailed studies wanting.

**Area:** Almost cosmopolitan.

**Limits:** The characteristic hairs separate this genus from other genera of cyphelloid

fungi. These hairs are inamyloid or more weakly amyloid than in *Lachnella* and the spores are likewise of a different type as compared with those of sect. *Lachnella*.

The limits between *Lachnella* and *Flagelloscypha* are difficult to draw, but the pseudoamyloid reaction of the everywhere thick walls of the hairs is here considered to be decisive. I cannot agree with the introduction of extension, density, or absence of crystal covering on the hairs or the pigment of their base or shape of their apices nor with the spore size and shape as a generic character in this group. Further crystallographic and chemical studies of the crystals and their development in each species would be necessary before this, frequently variable, character can be used and the acute or obtuse ending of the hair apices is often dependent on the age of these cells. Spore shape and size is not coordinated with other, more basic characters and is extremely variable in the *Crinipellinae*, especially *Crinipellis*. Agerer (1983, and in earlier papers) has attempted to solve the difficulties by introducing a rather narrow genus concept and, consequently, extraordinarily small genera which, it seems to me, are still, even so, rather heterogeneous in some instances. This is not to say that his taxonomy is not useful or that further studies may not eventually lead to the recognition of some of his taxa, or at least to a natural subdivision of the genus *Flagelloscypha*. Too few species have been studied for cyanophily of the spores. With at least one species of *Lachnella* having cyanophilic, and at least one of *Flagelloscypha* having acyanophilic spores, this character may become helpful in the delimitation.

*State of knowledge:* Aside from the species enumerated below, there are undoubtedly more taxa to be introduced in *Flagelloscypha* as defined here. The descriptions provided by Agerer (1975, 1979, 1980, 1983) are complete and instructive. He who identifies species should consult Agerer's treatments under *Flagelloscypha*, *Calathella*, and *Nochascypha* as well as *Recticipilus* and *Cephaloscypha*. I confine myself to the enumeration of nine species in the two groups as far as they have been studied by me.

*Practical importance:* Unknown. Several species are parasitic and may have some importance in plant pathology.

## SPECIES

### 1. Typical species (*Flagelloscypha* sensu stricto)

*F. minutissima* (Burt.) Donk; *F. citrispora* (Pilát) Reid (unless too close to the preceding species); *F. faginea* (Lib.) W.B. Cooke; *F. abieticola* (Karst.) W.B. Cooke; *F. polylepidis* Reid; according to Agerer also 14 other species.

### 2. Atypical species (with short or atypical flagelloid tips of the hairs or with subequal hairs with the crystalline covering reaching the tip, or the base of the hairs pigmented, or the apex of the hairs swollen, subcapitate).

*F. erucaeformis* (Batsch ex Fr.) Sing. (*Calathella*, Reid); *F. gayana* (Lév.) Sing.; *F. filicina* (Karst.) Donk; also *Cephaloscypha mairei* (Pilát) Agerer (*Cyphella*, Pilát; *Flagelloscypha morlichensis* W.B. Cooke).

Tribus *Myceneae* Fayod ex Ulbrich

*Ann. Sc. Nat. Bot.* VII. 9: 310. 1889 (Mycénés); Ricken ex Ulbrich in Maire, *Publ. Junta Cienc. Nat., Barcelona*, p. 56. 1933.

Type genus: *Mycena* (Pers. ex Fr.) S.F. Gray.

Syn.: *Marasmieae* subtrib. *Myceninae* Sing., *Lilloa* 22: 346. 1951.

*Hemimyceneae* Sing., *Sydowia* 2: 30. 1948.

*Fayodieae* Kühn., *Bull. Soc. Linn. Lyon* 49: 170. 1980.

**Characters:** Spores amyloid, or inamyloid; hyphae pseudoamyloid or inamyloid; cystidia present or absent, if present inamyloid; epicuticular elements never, not even partially pseudoamyloid, epicutis of variable structure; hyphae of the trama mostly with clamp connections in non-parthenogenetic forms; trama not reviving, monomitic, often many or almost all tramal elements strongly swollen and voluminous; hymenophore present or absent; if present lamellate or tubular; if the spores are inamyloid, the epicutis is usually with diverticulate hyphae and cheilocystidia are present, the base of the stipe is not insititious and the hyphae are strongly inflated or of two kinds (long voluminous and filamentous, intermixed - "sarcodimitic"); small white mycenoid or omphalioid fungi with basal mycelium belong here if they have diverticulate epicuticular hyphae and/or cheilocystidia; cystidia, pseudocystidia often present on the sides of the lamellae; basidia without carminophilous granulation; hymenophoral trama (if a hymenophore is present) more or less regular, not bilateral; collybioid or tricholomatoid carpophores with amyloid spores must have numerous dermatocystidia or an epicutis of short elements hymeniformly organized, or else the epicutis consists of extremely thin, smooth, filamentous hyphae or broadly rounded dermatocystidia filled with a dissolved grayish to fuscous intracellular pigment, otherwise habit always mycenoid or omphalioid; latex often present, but if present, mostly confined to the stipe; black rhizomorphy absent; on all kinds of substrata, sometimes parasitic, not ectomycorrhizal, not lichenized.

*Myceneae* is a tribus which is considered natural because it consists of an assembly of mutually related genera which seem to have their origin in certain groups of the Tricholomataceae and Leucopaxillaceae. Some genera and species resemble in habit *Gerronema*, *Tricholoma* and *Clitocybula* (see also under *Hydropus*).

KEY TO THE GENERA

- A. Hymenophore scarcely or not constantly or never developed; mature carpophores mostly with smooth hymenial surface. (See key II, p. 392).
- A. Hymenophore lamellate or tubular.
  - B. Spores with heterogenous wall or not quite smooth, either amyloid or inamyloid; heterogenous imbedded columns  $\pm$  cyanophilic; habit mostly omphalioid.\*  
106. *Fayodia*, p. 472
  - B. Spores with homogenous wall, acyanophilic.
    - C. Spores inamyloid.
      - D. Stipe with hyphae all inamyloid and not or scarcely metachromatic in cresyl blue mounts;

\*If mycenoid compare *Mycenella*, p. 356.

pileus and stipe neither viscid nor glutinous, nor lactescent, nor insititious nor soft-spinose or with cherocytes; small delicate mycenoid or omphaliod carpophores without pigment or with very little pigment (predominantly white, occasionally cream color); epicutis either with diverticulate or with conspicuous pilose bodies which are inamyloid; hymenophore lamellate, occasionally venose.

94. *Hemimycena*, p. 395

- D. Stipe, hyphae, pileus or epicutis different, or carpophores more strongly pigmented, or not mycenoid nor omphaliod.

E. Habit of the carpophores omphaliod to collybioid or pluteoid never bright red or pink nor with the stipe separated from the pileus by a separation zone nor with diverticulate nor with acanthophysoid elements in the epicutis; stipe never glutinous, never lactescent. If the trama of the pileus is at least partly a *Mycena*-structure (i.e. with very inflated, short hyphal cells), the center of the pileus is covered by tufts of dermatocystidia with intraparietal pigment (otherwise pigment most frequently vacuolar, rarely absent), or the hymenophore is poroid (consisting of very small, yellow pores) (see "H" below)

E. Habit of the carpophores mycenoid, more rarely omphaliod, often with bright colored pigments, stipe often separated from the pileus by a separation zone, or/and epicuticular elements hyphous or swollen and diverticulate; hypodermial and/or entire pileus trama with *Mycena* structure; if dermatocystidia are present, they do not occur in tufts restricted to the center of the pileus and do not have intraparietal pigment; stipe rarely glutinous or lactescent, rarely insititious hollow; hymenophore lamellate although often intervenose) (See "O" below: *Mycena* and *Amparoina*.

C. Spores amyloid.

- F. Hymenophore venose; pigments absent; development of the carpophores hemiangiocarpous (with a slight fugacious cortina in the type species, mostly bivelangiocarpous. hyphae inamyloid.

95. *Delicatula*, p. 397

- F. Hymenophore distinctly lamellate or tubular; development of the carpophores not bivelangiocarpous, rather rarely mono-velangiocarpous; pigments present or absent; hyphae inamyloid or pseudoamyloid.

G. Basal mycelium of the small to medium sized, frequently lignicolous and always pigmented carpophore fulvous, tawny, yellow; hyphal structure in cultures "textura angularis" or "textura epidermoidea" forming just behind the white, simple, primary mycelium (O.K. Miller 1971); rapid deep blue reaction with guaiac, strongly positive with tannic and gallic acid (O.K. Miller 1971); hyphae of the carpophores inamyloid, sometimes thick-walled and appearing glassy, or gelatinized, or turning red with KOH; habit of the carpophores omphaliod or collybioid, more rarely pleurotoid (but always stipitate, with decurrent lamellae, unless collybioid).

103. *Xeromphalina*, p. 424

G. Basal mycelium mostly white, rarely fuscous brown, rarely absent; the cultural characters indicated above different, or else not combining inamyloid hyphae with omphaliod or collybioid habit; collybioid carpophores must have either a pseudorrhiza or lilac pigment or the covering of the stipe is colorless and the basal mycelium white or at any rate not fulvous or yellow.

H. Hymenophore tubular with small pores. Tropical and thermophilous species; pigments not violet, lilac, or green; hyphae inamyloid, clamped; spores amyloid, rarely inamyloid; odor not raphanaceous; lignicolous; pores pallid, grayish, yellow, or pale pinkish.

100. *Filoboletus*, p. 419

H. Hymenophore lamellate (the lamellae may be intervenose, but then fung) not combining the characters enumerated above).

I. Habit collybioid; spores small; oleocystidia present on the sides of the lamellae and/or as cheilocystidia or dermatocystidia; lamellae crowded, narrow, free to adnate, mostly narrowly adnexed; stipe rarely eccentric, pruiniate; spores amyloid,  $<6 \mu\text{m}$ ; hyphae inamyloid; pigments clay color, brown, lilac, or almost none in the pileus. Lignicolous, or with a pseudorrhiza on conifer cones.

104. *Baeospora*, p. 426

I. Habit omphaliod or mycenoid, more rarely collybioid or even almost tricholomatoid, rarely pleurotoid; if collybioid, stipe not eccentric and not com-

- bining the characters indicated above or spores inamyloid; if pleurotoid, spores  $>6\ \mu\text{m}$ ; if with oleocystidia, trama hyphae pseudoamyloid.
- J. Epicutis hymeniform, of broad short elements; hyphae inamyloid; lamellae free or subfree; cystidia and cheilocystidia none; pigment intraparietal and/or incrusting; stipe not glutinous. 102. *Dermoloma*, p. 422
- J. Epicutis not hymeniform unless the fungus does not combine the other characteristics indicated above.
- K. Habit collybioid to almost tricholomatoid with narrowly adnexed to  $\pm$  deeply sinuate lamellae; pigment intraparietal and/or incrusting; dermatocystidia numerous on the pileus; stipe central rarely eccentric, hollow, stuffed, or solid; spores amyloid; hyphae inamyloid; on earth or rotten wood, under trees. 101. *Dennisiomyces* p. 421
- K. Habit rarely as above (and then not combining the characters indicated above), mostly omphalioid or mycenoid, rarely somewhat collybioid, pleurotoid or clitocyboid; pigment as above or more frequently intracellular (often vacuolar); spores amyloid or inamyloid; hyphae pseudoamyloid or inamyloid; on earth or on other habitats.
- L. Spores inamyloid.
- M. Center of pileus covered by tufts of long dermatocystidia which are large, with pigmented walls; a similar structure in the lower part of the stipe. Lignicolous, neotropical 96. *Pegleromyces*, p. 398
- M. Dermatocystidia, if present, different (see "N")
- L. Spores amyloid.
- N. Epicutis either consisting of a  $\pm$  discontinuous layer of single or bunched dermatocystidia with usually vacuolar pigment (or else without pigment) or of a thin layer of very thin, often pigmented (vacuolar pigment), smooth filamentous hyphae; hyphae of the trama rarely with *Mycena*-structure, or everywhere mostly filamentous, most frequently at least near hypodermium "sarcodimitic", i.e. partly filamentous but with numerous very long and broad elements intermixed, varying from (mostly) inamyloid to very weakly pseudoamyloid; pigment never bright red; stipe never glutinous, never with basal disc; habit mostly omphalioid, rarely more clitocyboid, collybioid, mycenoid or pleurotoid; most frequently gymnocarpous, rarely with a thin veil 99. *Hydropus*, p. 414
- N. Epicutis usually a cutis with often finely diverticulate hyphae, rarely with diverticulate cystidoid elements or disarticulating cherocytes (and then coarsely pruinate or soft-furfuraceous macroscopically); or more rarely the filamentous hyphae of the cutis or the elements of a hymeniform epicutis smooth but then spores amyloid and hyphae strongly pseudoamyloid (if inamyloid cf. also *Fayodia*)
- O. Cherocytes or multiseptate, thick-walled, diverticulate hyphae forming detersile spinules present and spores inamyloid; typically hymenial sporulation beginning when hymenophore still enclosed (margin affixed to stipe apex). 97. *Amparoina* p. 399
- O. If the epicutis is covered by a layer of cherocytes or detersile soft spinules, the spores are amyloid.
- P. Numerous oleocystidia present as dermatocystidia and cystidia; spores amyloid; hyphae pseudoamyloid no typical *Mycena*-structure. 105. *Resinomycena*, p. 427
- P. Not as above. 98. *Mycena*, p. 400

(Cyphelloid and other forms with smooth hymenial surface belonging to the Tricholomataceae)

- A. Sterile surface (surface of the pileus) not hymeniform; carpophores not consisting of a stipitate, hollow head with oleocystidia; spores always inamyloid.
- B. Trama partly or entirely gelatinized (if hymenophore strongly venose) see *Rhodoarrhenia*, p. 852
- C. Epicutis formed by smooth or lacerated elements; carpophores cyphelloid; spores not elongated. 71. *Stigmatolemma*, p. 344
  - C. Epicutis somewhat to strongly lacerate (a *Rameales*-structure, and astero stromelloid structure, or simply some coralloid, diverticulate hyphae or hairs present); habit or spores different.
    - D. Cups rising singly from the substratum, often ear-shaped (like *Otidea*), with a distinct pseudostipe; spores basically ellipsoid, tending to show a broad, spur-like, suprahilar bulge on the outer side (like many *Campanellas*). 72. *Aphyllotus*, p. 346
    - D. Cups densely aggregated; spores narrow. 70. *Stromatocyphella*, p. 345
- B. Trama not or scarcely gelatinized.
- E. Hyphae with clamp connections; special hair- or dermatocystidium-like bodies on sterile surface present (and then lacerate) or absent.
    - F. A true stipe, central or often  $\pm$  eccentric, well developed, pigmented below or darkening at maturity; hymenial surface quite smooth; spores smaller than  $10 \mu\text{m}$ , narrow; a strong *Rameales*-structure present, forming the epicuticular layer of the pileus; basidioles fusoid; trama hyphae mainly filamentous. Tropical.\* 61. *Cymatella*, p. 332
    - F. A true stipe absent, or it is strictly lateral and then generally white, a pseudostipe present or absent, sometimes nutant; not always combining the remaining characteristics enumerated above.
      - G. Pileus with nutant pseudostipe; trama of the stipe often  $\pm$  pseudoamyloid; spores more than  $10 \mu\text{m}$  long; hymenophore none or almost so. Tropical. 81. *Rimbachia*, p. 370
  - G. Fungi not combining these characters.
  - H. Trama of the pileus (cup) strictly monomitic, all or most hyphae filamentous and similar to each other, not or only weakly inflated (to  $12 \mu\text{m}$ ) in the middle zone of the trama, and/or pigment (if present) intraparietal and incrusting.
    - I. Stipe or pseudostipe present but lateral in mature specimens.
      - J. Growing on wood, earth or rock, often among *Nostoc*. Pigment none (or almost); spores up to  $8.3 \mu\text{m}$  long, ellipsoid (relatively broad); hymenial surface smooth, or a few lamellae exceptionally present. 62. *Skepperiella*, p. 333
      - J. Growing on earth or rock or on living Bryophyta; pigment dark, intraparietal, often incrusting; spores as above or different; hymenial surface veined, rarely lamellate and then anastomosing. (See "K" below).
    - I. Stipe none; pseudostipe present or absent, if present short and lateral to central; carpophores pendulous and cyphelloid or irregularly thin-expanded, membranous and without pigment or with intraparietal pigment, and bryogenous if the pseudostipe is lateral; rarely a stipe present and then pigment dark and intraparietal, incrusting.
      - K. Carpophore pileate or spatulate with hymenophore in form of veins, with intraparietal, often incrusting, dark pigment.
        - L. Pseudostipe long and nutant. 31. *Arrhenia*, p. 265
        - L. Pseudostipe short or absent, not nutant; generally growing on living mosses 32. *Leptoglossum*, p. 266
      - K. Carpophore cyphelloid or with a pigment-less, irregularly expanded membranous margin.

\*If stipe white and basidioles not fusoid, extratropical, see species of *Hemimycena* with poor development of hymenophore.

M. Spores very large and globose; sterile surface not with *Rameales*-structure; pigments present, incrusting; carpophores cyphelloid, normally with a short pseudostipe when mature. Temperate, on conifers

64. *Cyphella*, p. 335

M. Not combining these characteristics.

N. Carpophores cyphelloid, sometimes crowded and rising from a common stroma-like structure and often (but not always) pigmented; *Rameales*-structure generally distinct.

66. *Calyprella*, p. 337

N. Carpophores not or only initially cyphelloid, eventually expanded into rather flat, irregular membranous pigment-less carpophores which mostly grow on living mosses and may eventually produce a few lamellae; *Rameales*-structure often very weak and intermittent and/or restricted to the rim of the margin; never growing on a common stromatic base. Often on living mosses.

63. *Mniopetalum*, p. 334

H. Trama of the pileus of both filamentous and broad, voluminous elements as often seen in *Hemimycena*, or with approximately a *Mycena*-structure (multiseptate, voluminous hyphal cells); pigment often practically absent or yellow, not incrusting (cf. "Q")

108. *Pleuromycenula*, p. 432

E. Either clamp connections absent in the carpophore, or special epicutis elements with pseudoamyloid appendages or warts or hair- or cystidium-like bodies differentiated on the sterile surfaces, and these surface hairs not lacerate-ramose but long and much like those of *Crinipellis* and *Chaetocalathus*; if surface structures are cystidioid, they are diverticulate as in *Mycena* or like the acanthocysts of *Favolaschia*.

O. Pileus with a distinct intraparietal mostly incrusting pigment, gray, fuscous, or fuliginous; hymenophore generally veined, rarely lamellate and then lamellae anastomosing; special hairs absent; *Rameales*-structure not present on the sterile surfaces (see "L" above: *Leptoglossum*)

O. Pileus different; hymenophore not developed or scarcely so.

P. Sterile surface hyphous or with dermatocystidioid hairs or with a *Rameales*-structure, but mostly without well differentiated hairs; epicutis a cutis or a trichodermium; clamp connections absent; if hairs present - spores <8 µm.

Q. Hyphae and dermatocystidia with an acanthocyst-like diverticulation (as in *Mycena* or *Favolaschia*); pigments none. Neotropics. 109. *Mycoalvicia*, p. 433

Q. Surface elements of the pileus without a diverticulation of the type described above; pigments present or absent.

R. Sterile surface of pileus a *Rameales*-structure; stipe present (see "F" above).

R. Sterile surface of pileus with a very weak, intermittent *Rameales*-structure, or without a *Rameales*-structure; stipe absent (pseudostipe present or absent).

S. Sterile surface - a trichodermium; cystidia present or absent.

41. *Cyphellostereum*, p. 286

S. Sterile surface - a cutis; cystidia none.

65. *Phaeodepas*, p. 336

P. Sterile surface always with long hairs which are well differentiated, often ± pseudoamyloid, often partly or entirely crystalliferous-incrusted, or apically subcapitate; hyphae usually with clamp connections (in one species, *Calathella columbiana* Agerer, see under *Flagelloscypha*, known to be clamp-less but here spores >10 µm, hairs weakly pseudoamyloid).

T. Hairs distinctly pseudoamyloid, thick-walled, mostly rising from a ± well defined hypotrichium or at least sharply separated from the trama, thick-walled, throughout, not becoming thin-walled and flagella-like-acute in the upper portion, of nearly equal diameter from base to apex or gradually slightly narrowing towards a rounded tip (or at least the majority so), hyaline (pigmentless), densely covering the entire sterile surface and covering the primordial hymenium in the early stages; hyphae with clamp connections

92. *Lachnella*, p. 386

T. Hairs varying from weakly pseudoamyloid (except at the apex) to inamyloid, or

with acute or subacute or suddenly swollen thinwalled apex, all hyaline or in the basal portion somewhat pigmented, or else hairs replaced by several strongly pseudoamyloid flagella-like appendages rising directly from the uppermost cells of the hypotrichium; hyphae with, more rarely without clamp connections.

U. Long hairs constantly present, not appendiculate; strongly pseudoamyloid flagella-like or verrucose appendages absent in all cells.\*

V. Hairs ± incrusted.

93. *Flagelloscypha*, p. 387

V. Hairs never incrusted, most of them always capitate, with thin to firm, in no part thick walls. Pigments none.

107. *Cellypha*, p. 431

U. Long hairs absent but surface cells appendicated or with verruciform tips which are strongly pseudoamyloid.

91. *Amyloflagellula*, p. 385

A. Sterile surface hymeniform or carpophores consisting of a hollow stipitate head and then with oleocystidia, or spore amyloid (see key III)

### KEY III

AA. Spores amyloid (see key I "B", usually *Mycena*).

AA. Spores inamyloid (all Marasmiinae).

BB. Pilus head-like, hollow, bearing hymenium on the outside (with areas directed away from the substratum sterile or substerile), or long-clavate and somewhat clavarioid, the sterile portions of the head and the pseudostipe hymeniform, more rarely subhymeniform (elements not crowded); oleocystidia usually present and numerous; other cystidia often also present; trama always very thin, inamyloid in the head-portion.

82. *Physalacria*, p. 372

BB. Pilus normally developed or carpophores ± cyphelloid; sterile surfaces generally well separated from the hymenial surface; oleocystidia present or absent.

CC. Epicuticular elements all or mostly broom cells.

DD. Carpophores cyphelloid, often with pseudostipe; hymenophore venose to scarcely lamellate or nil; oleocystidia present, these often large and/or with short finger-like appendages at the apex (see "HH" below).

DD. Carpophores stipitate, agaric-like; oleocystidia generally absent in non-lamellate forms.

EE. Hyphae of the trama all inamyloid; black rhizomorphs present

86. *Manuripia*, p. 378

EE. Hyphae pseudoamyloid or black rhizomorphs absent.

FF. Stipe central; black rhizomorphs present or absent. 87. *Epicnaphus*, p. 378

FF. Stipe inconspicuous and lateral; white rhizomorphs present or absent (see *Marasmius*).

CC. Epicuticular elements smooth.

GG. Characteristic dermatocystidia present; capitate cystidia and/or dermatocystidia, oleocystidia, or hair-like cystidia or metuloids mostly present.

HH. Carpophores cyphelloid, often with pseudostipe, or else sessile; stipe and hymenophore absent, or the latter present, a few anastomosing lamellae or veins; oleocystidia present.

83. *Deigloria*, p. 373

HH. Carpophores more agaricoid with stipe; hymenophore lamellate to smooth; oleocystidia present or absent.

84. *Gloiocephala*, p. 375

GG. Dermatocystidia and well differentiated cystidia absent.

\*If the hairs are entirely or for the larger part non-incrusted and pigmented and the pilose surface layer not sharply separated from the trama and the spores sometimes tending to brownish in age, or if the hairs are ramosely divided, or if the basidia are short, subspheroid-clavate or with cross walls (tremelloid), or if the hymenium is covered at maturity in a marine fructification, the fungi are not keyed out in this key, but see the genera *Cyphelopsis*, *Rectipilus*, *Halocyphina*, *Henningsiomyces*, *Merismodes*, *Phaeocyphelopsis* (p. 111). The relationships of these genera are not necessarily with the Tricholomataceae, Agaricales.

- II. Carpophores medium to large, with long central stipe and smooth hymenial surface; pigments bright colored. 88. *Hymenogloea*, p. 379
- II. Carpophores minute without bright colors.
- JJ. Abundant basal mycelium demonstrable. 85. *Palaeocephala*, p. 377
- JJ. Stipe insititious (cf. *Marasmius*, sect. *Epiphylli*).

#### 94. HEMIMYCENA Sing.

*Rev. de Mycol.* 3: 194. 1938.

Syn.: *Perona* Pers., *Mycol. Eur.* 2: 3. 1825, non *Peronia* F.d.l. Roche in *Redouté* 1811.

Type species: *H. lactea* (Pers. ex Fr.) Sing.

**Characters:** Habit mycenoid or omphaloid, stipe rarely eccentric; pileus and stipe mostly white, rarely with a faint shade of ocher on disc or base, generally thin, almost membranous, not reviving, delicate, putrescent, subhygrophanous to hygrophanous; lamellae generally well formed, even broad, to very broad, or narrow to venose, ascendant or horizontal to descendent; spore print white (or pale cream?); spores hyaline, thin-walled, smooth, varying from short ellipsoid to cylindric or fusiform, very frequently elongated or ventricose-fusoid, inamyloid; hyphae of the stipe inamyloid not distinctly metachromatic in cresyl blue mounts; cheilocystidia generally present; cystidia on sides of lamellae often present; stipe in youth or age not separated from the pileus by a sudden decrease of hyphal volume or by an apical separation layer; hymenophoral trama regular or subregular, vaguely gelatinized or densely compacted, trama of pileus of large-celled as well as filamentous, somewhat interwoven hyphae and in some species with long and broad hyphae intermixed ("sarco-dimitic" pileus and stipe not glutinous; apex of stipe not pigmented; base of stipe never quite insititious (although only a few basal fibrils may be present) nor with basal disc; laticiferous hyphae in pileus not present; hypodermium not strongly differentiated by the size of the hyphal elements, i.e. hypodermal elements not consistently short and voluminous at least in the species with mycenoid habit and non-decurrent, ascendant lamellae and even in these little differentiated from an epicutis layer of more filamentous repent hyphae. On various plant débris.

**Development of the carpophores:** Probably, at least in most cases, gymnocarpous or almost so, but Reijnders (1963) adds for *H. mauretanica* "(or monovelangiocarpous)".

**Area:** Very widely distributed, probably almost cosmopolitan.

**Limits:** *Hemimycena* had originally been conceived as a subgenus of *Mycena* in the same sense as Kühner's *Paramycena* which was merely a receptacle for all the species of *Mycena* in the wider (Kühner's) sense with inamyloid spores. It has since then undergone a gradual change and is now basically the same as the genus *Delicatula* of Kühner & Romagnesi (thus recognized as an autonomous genus), without however, the type species of the genus *Delicatula* and without "*Mycena*" *quisquiliaris* (Josserand) Kühner, but with the "group" *Lacteae* Kühner which by gradual transitions passes over into "these white Mycenas and white Omphalias which we have for

convenience sake assembled under the name of *Delicatula*" (Kühner & Romagnesi 1953). It is obvious that, with this circumscription, the genus *Hemimycena* is a natural genus and moreover one that ought to be separated from *Mycena* even if species with inamyloid spores are admitted in the latter. If *Hemimycena*, *Xeromphalina* and *Hydropus* are not separated from it - all of these now large genera - *Mycena* becomes an unwieldy, unnatural giant genus, impossible to define properly. Between the white species of *Mycena* with inamyloid spores, as far as they are now known, and the Hemimycenas (those that were included in *Delicatula* by Kühner & Romagnesi 1953) there is a clear hiatus both chemically and structurally since the former have (1) weakly amyloid or at least distinctly metachromatic stipe trama in cresyl blue mounts, at least in the cortical layer (2) typically more or less differentiated hypodermium and/or a supralamellar layer, regular hymenophoral trama of short swollen elements, insititious stipe or basal disc, blue pigment, glutinous layers on pileus and/or stipe surface, a separation layer between the trama of the stipe and the trama of the pileus, etc.

In practice, it occurs much more frequently that *Hemimycena* is difficult to distinguish not from *Mycena* but from *Marasmiellus*. But if centrally stipitate mycenoid or omphalioid or collybioid agarics without pigment have a distinct basal mycelium, they can be inserted in *Hemimycena* with confidence unless they have such special characteristics (a gelatinized zone in the trama, setoid dermatocystidia or clampless hyphae) as are exclusive for some section of *Marasmiellus*.

Since the stipe of the Hemimycenas is permanently central or almost so, and the hymenophore developed at least in form of veins or late-forming lamellae, neither *Marasmiellus* section *Marasmiellus* nor any of the reduced genera (including *Pleuromycenula*) should be confused with *Hemimycena*. It should also be taken into consideration that species with reviving context (after desiccation) do not belong in *Hemimycena*, and that species with small short spores and a voluminous hilar appendage, or species with non-smooth or heterogenous spore wall do not enter this genus.

Some of the species of *Hemimycena* enter Corner's concept of *Trogia* (see there).

Kühner and Kühner & Romagnesi treat in this group likewise a species which I have studied only superficially and which does not have a differentiated epicutis of the pileus or cystidia or cheilocystidia. This is *Omphalia ignobilis* which in the past I considered as belonging in *Clitocybe* where it was the type of a section without, apparently, close relationships with other species of that genus. At present I consider the position of this species as uncertain until future discoveries and a more detailed study of the species in question give a hint as to a systematically more satisfactory solution. If the naked base of the stipe as described by these authors means insititious stipe, it might be better to keep it separate from both *Clitocybe* and *Hemimycena*.

*State of knowledge:* The Hemimycenas have only recently found some more attention among modern mycologists, especially as a consequence of the work done by Josserand (as *Omphalia*) and later by Kühner, Smith and Redhead. 26 species are here recognized but it may be assumed that there are many more of these

frequently overlooked fungi still not sufficiently studied in all respects and hiding in the world literature as Omphalias, Mycenas, Delicatulas, etc., or even as cyphelaceous species, especially as far as the flora of Asia and Australia is concerned.

*Practical importance:* Unknown.

## SPECIES

*H. cucullata* (Pers. ex Fr.) Sing. [Agaricus, Pers., Fr.; Mycena gypsea (Fr.) Gillet sensu Ricken; Hemimycena Sing.; Marasmiellus, Sing.]; *H. rickenii* (A.H. Smith) Sing. (Agaricus lacteus var. pulchellus Fr.); *H. patagonica* Sing.; *H. delicatella* (Peck) Sing. [Collybia, Sacc.; Hemimycena lactea (Pers. ex Fr. sensu Lange) Sing.; Mycena, Kummer; Mycena ludia (Fr.) sensu Ricken; Mycena lactea var. pithya (A. & S. ex Fr.) Quél. sensu Pat.; Mycena crystallina Peck]; *H. pseudolactea* (Kühner) Sing. (Mycena, Kühner; Marasmiellus, Sing.); *H. albida* (Murr.) Sing. (Gymnoporus, Murr.; Marasmiellus, Sing.); *H. angusta* Sing.; *H. epibiotica* Sing.; *H. crispuliformis* Sing.; *H. setulosipes* (Murr.) Sing.; *H. herrerae* Sing.; *H. praedecurrents* (Murr.) Sing.; *H. truncicola* Sing.; *H. cephalotricha* (Josserand ex Redhead) Sing.\* (Omphalia, Josserand; Mycena, Kühner; Marasmiellus, Sing.); *H. gracilis* (Quél. sensu Sacc.) Sing. (Mycena, Kühner; Omphalia, Quél.); *H. pseudogracilis* (Kühner & Maire) Sing. (Mycena, Kühner & Maire); *H. crispata* (Kühner) Sing. (Mycena, Kühner); *H. candida* (Bres.) Sing. (Omphalia, Bres.; Mycena, Kühner; Marasmiellus, Sing. 1951); *H. delectabilis* (Peck sensu A.H. Smith) Sing. (Mycena, Sacc.); *H. mairei* (Gilbert) Sing.; (Omphalia, Gilbert; Mycena, Kühner); *H. pseudocrispula* (Kühner) Sing. (Mycena, Kühner); *H. subtropicalis* Sing.; *H. crispula* (Quél. sensu Kühner) Sing. (Omphalia Quél.; Mycena, Kühner) (= *H. hirsuta* acc. to Redhead, see below); *H. mauretanica* (Maire) Sing. (Omphalia, Maire; Mycena, Kühner); *H. epibrya* Sing.; *H. angustispora* (Josserand ex Orton) Sing. (Omphalia, Josserand; Mycena, Kühner). Obviously also *H. epichloe* (Kühner) Sing. (Mycena, Kühner); *Mycena albicolor* A.H. Smith, *M. setulosa* A.H. Smith and other species of the evidently artificial section *Deminutivae* Smith; obviously *H. hirsuta* (Tode ex Fr.) Sing.\*\* (Delicatula gibba (A. & S. ex Pers.) Kühner sensu Patouillard); perhaps *Marasmiellus buccinulus* (Speg.) Sing. [non *Hygrophorus buccinulus* (?Speg.) Dennis sensu Dennis], *M.(H.) longicystis* Heim, *H. brevispora* Pegler, and *Helotium nebulophilum* Redhead.

## 95. DELICATULA Fayod

*Prodrome...*, Ann. Sc. Nat. VII. 9: 313. 1889.

*Type species:* *D. integrella* (Fr.) Pat.

*Syn.:* *Retocybe* Velen., Nov. Myc. Nov., p. 33. 1947.

\*c.n. (*Helotium cephalotrichum* Joss. ex Redhead, Can. J. Bot. 60: 2004, 1982).

\*\*c.n. (*Helotium hirsutum* Tode ex Fr., Syst. Myc. 3: 94. 1829; Redhead l.c. p. 2007).

**Characters:** Habit of the carpophores mycenoid-omphaliod, small and slender, almost transparent, hygrophanous, pigmentless; pileus at first with a velar layer consisting of thick-walled hyphae; epicutis - a thin layer of thin-walled, filamentous, repent hyphae; hypodermium made up of somewhat thicker, radially arranged hyphae and proliferating beyond the margin if the pileus forming thin filamentous appendages; hymenophore often reduced to mere veins (especially in immature or retarded specimens), otherwise consisting of narrow lamellae; spores hyaline, subamygdaliform-ventricose, smooth, amyloid, with thin homogeneous wall; basidia normal; cystidia none; hyphae of the trama inamyloid, subregularly arranged in the hymenophore, with numerous clamp connections. On débris and sticks, logs, etc.

**Development of the carpophores:** Hemiangiocarpous (see Kühner, 1926, p. 96); according to Reijnders (1963) monovelangiocarpous or bivelangiocarpous but the lipsanenchyma is an outgrowth which extends during the whole primordial phase; pileostipitocarpous.

**Area:** Unknown, probably widely distributed.

**Limits:** This genus differs from all other genera by its veil, the amyloid spores, the hemiangiocarpous development of the carpophores and the structure of the cuticle of the primordia, also by the lack of all kinds of pigment. It has the appearance of *Hemimycena* but can be distinguished easily by the amyloid spores.

**State of knowledge:** Only two species have been studied thoroughly (Kühner, Josserand, Singer), but there are more.

**Practical importance:** None.

## SPECIES

*D. integrella* (Fr.) Pat.; according to Maire and others also *D. cuspidata* (Quél.) Cejp; certainly *Retocybe millaria* Velen. (type seen, but possibly identical with some other species); perhaps also *D. craticula* Heim and *D. minima* Sing. (ined.).

## 96. PEGLEROMYCES Sing.

*Mycologia* 73: 500. 1981.

**Type species:** *P. collybioides* Sing.

**Characters:** Habit collybioid; epicutis little developed but a seemingly velar stratum in the center of the pileus and at the base of the stipe well developed, consisting of dermatocystidia which are in places densely and subhymeniformly arranged, 50-70 × 8-21 µm in the type, characteristically brown from an intraparietal and incrusting pigment; hypodermium - a cutis of subparallel hyphae which are smooth above but also pigmented as the velar layer; cystidia present; hyphae short-celled and cells voluminous (Mycena-structure) in the lower layers of the trama of

the pileus, all hyphae inamyloid, non-gelatinized, with clamp connections, and pigmentless (excepting those of the cortical layers); lamellae adnexed to subadnate, hymenophoral trama regular; spores hyaline, smooth, inamyloid, uni-nucleate, acyanophilic, rather small and short ellipsoid; stipe central, not insititious. On logs in the tropics.

*Development of carpophores:* This has not been studied in detail, but apparently "hemiangiocarpous" (velangiocarpous).

*Area:* Neotropics (Amazonas).

*Limits:* This genus differs from the inamyloid-spored sections of the genus *Mycena* in the structure of the surface layers of both pileus and stipe. It differs from *Hemimycena* in the pigmentation and the lack of strictly epicutis-like layer(s) on the margin of the pileus and the dermatocystidial layer in the center and at the base of the stipe. *Hydropus*, at least its species with inamyloid spores and trama, is structurally completely different, and the dermatocystidia have normally only vacuolar pigments. *Pegleromyces* also differs from *Marasmius* sect. *Alliacei* in the characteristics of the covering of pileus and stipe and the *Mycena*-type tramal structure.

The dermatocystidia of the pileus and the base portion of the stipe are here tentatively interpreted as velar in origin, but studies of the development of the primordium have not been available to prove this. If these dermatocystidia were part of an epicutis disintegrating during later development, the distribution of this layer, its pigments, and its occurrence together with a *Mycena*-type tramal structure would be sufficient to separate this new genus from others.

*State of knowledge:* Only the type species is known.

*Practical importance:* Unknown.

## SPECIES

*P. collybioides* Sing.

### 97. AMPAROINA Sing.

*Mycologia* 50: 110. 1958.

*Characters:* Habit mycenoid (but tending somewhat to gastroid), with central stipe which is somewhat columelliform in young stages, insititious or subinsititious, with the margin of the pileus at first attached to the apex of the stipe; lamellae narrow, subfree; spores hyaline, smooth, medium sized, inamyloid, acyanophilic; basidia subhymeniform to hymeniformly arranged, often early collapsing, usually sporulating at a stage when the hymenophore is still enclosed, with nearly half-sickle-shaped sterigmata but some of these occasionally filiform; hyphae inamyloid or pseudoamyloid; covering of pileus and stipe detersile, soft-spinose, the spinules consisting of subisodiametric to elongated, often diverticulated cells, some of them dissociated (cherocytes). On dead wood.

**Development of the carpophores:** In the earliest stages seen, the hymenium is enclosed. These species are certainly not gymnocarpous, but primordia not studied in detail.

**Area:** Known from the American subtropics and tropics (lowland tropical forests of Colombia) and from New Caledonia.

**Limits:** The Amparoinas are similar to the Mycena of section *Basipedes* but have inamyloid spores. They are easily separable from other genera of the Mycenae, particularly the related genera *Hemimycena*, *Delicatula*, *Pegleromyces* and *Mycocalvinia*. The main problem is the interpretation of this genus. It was when first collected interpreted as a first step towards bulbillosity (Singer & Digilio 1951). Later, as the more gasteroid *A. heteracantha* was discovered, the genus was considered secotoid inasmuch as there seemed to be a certain similarity with *Hemigaster*, but it is now rather doubtful that *Amparoina* can be considered to be secotoid since Horak (1980) says he has obtained a (white) spore print from material collected near the type locality of *A. spinosissima*. This does not rule out that the Amparoinas may be understood as the beginning of gasteromycetation of certain groups of Mycenes (*Basipedes*) whereby the spores borne on enclosed hymenia are inamyloid. On the strength of Horak's observation *Amparoina* is now reinstated in the Tricholomataceae (Agaricales).

**State of knowledge:** Two species are completely known.

**Practical importance:** Unknown.

## SPECIES

*A. spinosissima* (Sing. in Sing. & Digilio) Sing.; *A. heteracantha* Sing.

### 98. MYCENA (Pers. ex Fr.) S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 619. 1821.

**Type species:** *Mycena galericulata* (Scop. ex Fr.) S.F. Gray.

**Syn.:** *Agaricus* sg. *Mycena* Pers. ("sectio") ex Fr. ("tribus"), *Syst. Myc.* 1: 140. 1821.

*Helotium* Tode ex Leman in *Dict. Sc. Nat.* 20: 507. 1821, June 29 non *Helotium* (Pers.) ex St-Amans, *Fl. Agen.* p. 529, 1821, 20-28 April (Ascomycetes); Fr., *Syst. Myc.* 2: 155. 1823.\*

\**Helotium* Tode in the original sense and as validated by Leman is based on the lectotype (Donk) *H. glabrum* which is most probably a young stage of *Mycena capillaris* as Fries himself suggested. Other interpretations are not fully impossible (*Marasmius*, *Marasmiellus*, *Mycena polyadelpha*, and even *Cudoniella* have been suggested). Redhead (*Canad. J. Bot.* 60: 1998-2013. 1982) gave the most detailed account of the history of *Helotium* but I cannot agree with him on three important points: (1) Donk's choice of lectotype is by no means to be rejected as arbitrary but on the contrary, *must* be accepted (Art. 8.1) since it is not in serious conflict with the protologue (Tode) nor was it based on a largely mechanical method of selection. (2) If Fries 1825 indeed indicated a nomenclatorial type, it was based on the assumption that *Perona* is a nomen novum for *Helotium* Tode which it is not, and "*H.*" *gibbum* was not

*Gymnopus* (Pers. ex) S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 604. 1821.\*

*Mycenula* Karst., *Medd. Soc. Faun. Fl. Fenn.* 16: 89. 1889.

*Prunulus* Caes. ex S.F. Gray sensu Earle (Murr., non Sing. & Sm.) *Bull. N.Y. Bot. Gard.* 5: 427. 1909.

*Insiticia* Earle, l.c. p. 425.

*Basidopus* Earle, l.c., p. 426.

*Collopus* Earle, l.c.

*Galactopus* Earle, l.c.

*Stereopodium* Earle, l.c.

*Linopodium* Earle, l.c.

*Poromycena* Van Overeem in Van Overeem & Weese, *Icon. Fung. Malay.* 14-15: 4. 1926.

*Pseudomycena* Cejp, *Publ. Fac. Sc. Univ. Charles*, p. 138. 1930.

*Leiopoda* Velen., *Nov. Noviss. Op. Bot. Czech.* 4: 35. 1947.

*Zephirea* Velen., l.c., p. 61 p.p. (see p. 804).

*Corrugaria* Métrod, *Les Mycènes de Madagascar*, p. 127. 1949.

*Phlebomycena* Heim, *Rev. d. Mycol.* 10: 26. 1945 ex Heim, *Rev. d. Mycol.* 31: 23. 1966.

?*Hiatula* (Fr.) Mont., *Ann. Sc. Nat.* IV. 1: 107. 1854.

?*Leptomyces* Mont., *Syll. Gen. Spec. Crypt.*, p. 128. 1856.

?*Leucoinocybe* Sing., *Ann. Mycol.* 41: 144. 1943 ad int.

**Characters:** Habit of the carpophores mycenoid or omphaloid (in the latter case epicutis of the pileus never consisting of smooth filamentous hyphae); pigment present or absent, bright colored, or dull colored; pileus usually thin and pellucid,

one of the original species of *Helotium* Tode. (3). Fries (1832) merely mentions *Helotium* Tode as “de loco incerto in *Syst. omisi.*” Since “omitted” is the exact opposite of “adopted” (the word used in Art. 13d of the 1983 Code), this mention cannot supersede *Helotium* Tode ex Leman even if *Helotium* Tode ex Leman were not a later homonym of *Helotium* (Pers.) ex St-Amans, “sanctioned” by Fries as a subgenus. It must be admitted that Korf’s interpretation of the Sydney rules seems to accept any mention by Fries, *Systema + Index + Elenchus* as “sanctioning”. If so, the Sydney Code, aside from all its victims on the specific level, might cause the nomenclaturist to abandon *Mycena* in favor of *Helotium*, with hundreds of species to be transferred to the latter, a situation which would undoubtedly lead to an eventual conservation of *Mycena* - after at least ten years of nomenclatorial uncertainty.

It appears that *Mycena* is not the only genus of Basidiomycetes that is in danger of being abandoned in favor of pre-Friesian names if the Sydney Code is applied. The proposals to conserve *Amanita*, *Clavulinopsis*, *Coriolus*, *Delicatula*, *Gloeophyllum*, *Gyrodon*, *Lactarius*, *Lentinus* (this is clearly unnecessary, cf p.183) *Leptoglossum*, *Phellinus*, *Pulcherricum*, *Pycnoporus*, *Spongipellis*, *Volvariella* (*Taxon* 33: 730-736. 1984) and the changes of lectotypes and author citations for example in *Suillus* (*Taxon* 33: 711-712. 1984) are proof of the fact that the thoroughly negative impact on Basidiomycete nomenclature caused by the rule changes at Sydney is far from the statements made by their promotors, and that these changes can be avoided by accepting proposals 42-44 (*Taxon* 33: 745-747. 1984). This latter solution is preferable to the conservation of all the separate taxa afflicted because it settles the problem uniformly, avoids the otherwise unavoidable discussions about the meaning of pre-Frisian taxa published in books not available in most institutions where taxonomical research on Basidiomycetes is carried out and the - necessarily controversial - designation of neotypes for these taxa. It will also help to put an end to the interminable rule changes from Congress to Congress (cf. Machol. *Taxon* 33: 532-533. 1984) which have contributed to counteract the very purpose of the International Code of aiming “at the provision of a stable method of naming taxonomical groups” (Preamble 1).

\*The type species of *Gymnopus* is *G. purus* (Pers. ex) S.F. Gray. Earle took up, as type species, *Agaricus longipes*. Since both S.F. Gray’s and Earle’s genus are originally based on the same section, Donk thinks they should both have the same type. Since Persoon’s treatment of *A. longipes*, again according to Donk, does not justify Earle’s typification, the type of both genera would have to be *G. purus*. If, however, *Gymnopus* (Pers.) Roussel ex Earle is taken as a different genus, with the type designation as given by Earle, this latter genus would be a later homonym of *Gymnopus* (Pers. ex) S.F. Gray and a later synonym of *Oudemansiella*.

striate; epicutis of the pileus usually consisting of diverticulate (Pl. 38), filamentous or elongate and irregular hyphae, much more rarely these diverticulate hyphae spherocystoid or hair-shaped (Pl. 61, ep) or they are filamentous but smooth, or they are globose and smooth (*M. rorida*-group); if the epicuticular hyphae are smooth the spores are distinctly amyloid; or else the trama is pseudoamyloid or else there are numerous lacticiferous hyphae, or pileus and stipe strongly glutinous, or stipe insititious, or at least a hypodermial layer well differentiated with voluminous short elements ("Mycena-structure") which also usually show in the hymenophoral trama (which is regular), and in a supralamellar layer (immediately above the lamellae); also in the species with distinctly diverticulate epicuticular elements, generally the hypodermium and subcutis more or less individualized, one of the layers underneath the epicutis often gelatinized (then the pileus viscid), or consisting of large, short elements (Pl. 38) (subcellular); hymenophore usually distinctly lamellate; lamellae ascendant, horizontal or descendant, subfree to decurrent, rarely developing late showing as smooth to venous hymenial surface in young or retarded carpophores; hymenophoral trama subregular to regular or almost subcellular (consisting of rather large and short elements), often strongly pseudoamyloid, rarely practically inamyloid, base of stipe - a pedestal in form of a disc, or with a pseudorrhiza, or with fibrous to woolly basal mycelium, or insititious; covering of stipe little differentiated to analogous to that of the pileus or with dermatocystidia or hairs (Pl. 41, 61 st; 62, 3 dc); spore print white to pale cream; spore wall hyaline, homogeneous, smooth, thin, acyanophilic (see also Pl. 50, 1-3, 5); basidia normal, but often 1-3-spored as well as 4-spored; cheilocystidia present, other cystidia also often present; stipe central sometimes with latex (with numerous lacticiferous hyphae), usually very thin, fragile to subcartilaginous, usually tubulose; veil none, rarely cortinoid; cherocytes (*Cryptog. Mycol.* 4, pl. 1. 1983) often present; context not reviving; tissue of the stipe most frequently at least weakly pseudoamyloid; hyphae with numerous clamp connections, at least in the "normal", i.e. non-parthenogenetic races; rarely, especially in section *Radiatae*, with irregular or rare clamp connections; carpophores attached to the substratum (bark, living or decaying wood, Pteridophyta, moss, dead needles or foliage, charcoal, cones, sticks, humus and sand, or other kinds of soil), rarely (sect. 5) a stilboid generation on living leaves; mycelium not ectomycorrhizal, without connection with black rhizomorphs, often luminescent.

*Development of the carpophores:* Stipitangiocarpous in *M. longiseta*, *M. stylobates*, *M. bulbosa*; pilangiocarpous in *M. epipterygia*, *M. galopoda*; mixangiocarpous in *M. osmundicola*, *M. inclinata*. If specialized hairs on the surface of the primordia are interpreted as a transformed universal veil (see chapter XI, XII) many species must be interpreted as monovelangiocarpous, e. gr. *M. tenerrima*, *M. osmundicola*, *M. quercusilicis*, *M. capillaris*, *M. pterigena*, *M. sanguinolenta*. The rest of the species studied are either gymnocarpous (certainly so *M. semivestipes* according to the studies of Douglas and *M. rorida* according to Reijnders). All species are either pileostipitocarpous or stipitocarpous (Reijnders). The different categories of development types do not coincide with the accepted sections.

*Area:* Almost cosmopolitan.

**Limits:** As for *Hemimycena* see that genus. *Delicatula* can be easily distinguished by the coordinated characters of the latter genus; there are however, some species which are very similar to *Delicatula* but lack the velar covering of that genus. These (thus far unpublished, all tropical) have been interpreted as *Mycena* for the time being, especially if there are weakly pseudoamyloid hyphae in the stipe, or normal, broad, non-decurrent lamellae or both. *Hydropus* which has been incorporated in *Mycena* by some authors is clearly different from *Mycena* by the key characters (see also under *Hydropus*) and it may be generally stated that *Mycena* differs from other genera of this tribus by the characters outlined in the keys. As far as the species now enumerated are concerned, there are hardly any appreciable difficulties of delimitation to be expected - if all characters mentioned in the keys and the generic and sectional descriptions are carefully studied - but the still large number of species thus far nor sufficiently studied in all these particulars and the numerous exotic species still unknown may (or may not) introduce new problems in the future.

Some species of *Mycena*, mainly of tropical origin, now well known and fully described, come so close to the description of *Hiatula* and *Leptomyces* that we now doubtfully include these genera in the synonymy list of *Mycena*. As for *Hiatula* which has been interpreted as a ringless *Leucocoprinus* by some authors, see also under Agaricaceae (p. 511). The types of the species referred originally to *Leptomyces* by Montagne have been searched for in Paris but they do not seem to exist any more. While it is undoubtedly true that the diagnoses of both *Hiatula* and *Leptomyces* may still be interpreted in various ways, and no proof can be offered for the preference of this author, it is equally true that the separation of *Mycena* from *Leucocoprinus* does not present any taxonomical problem.

**State of knowledge:** The general knowledge of the species of *Mycena* is much better than the somewhat confused nomenclatorial situation may suggest. In this regard, the ratio between the state of knowledge on one hand and the disagreement about some names on the other are comparable in *Mycena* and *Russula*. In both genera three monographs have been published, all based on modern research methods, but the older names are often interpreted in different ways.

It appears to this author that in the matter of European species concepts, material collected only in America, or for that matter in any non-European region, is not decisive. While some of Smith's reasons for different interpretations seem, at least to the non-specialist, quite convincing, they often are difficult to accept because of European traditions, and European phytogeographic considerations. Under these circumstances, it seems to be correct to adopt a certain definite policy as to the acceptance or non-acceptance of names in *Mycena*, or else two nomenclatorial schools will perpetuate themselves. The author believes that if tradition and text of the Friesian diagnosis is not clearly and undoubtedly on the side of one author, then, in case of disagreement, the names involved should be considered as "nomina dubia". Without regard as to whether or not future taxonomists will have a list of nomina dubia in *Mycena* (and other genera with a similar nomenclatorial situation) at their disposal, these names are here disregarded, and newer binomials are substituted. If a European species is interpreted by only one author without disagreement on the

side of any other modern author, this interpretation is here accepted, but the words "sensu X" are added to the binomial. This is more risky if the modern material comes from America. In the latter case the author is rather pessimistic about the final outcome. Such "tele-interpretations" take it for granted that there is no difference in the mycological flora of Europe and the temperate zone of North America, and that all species occurring in this country must also occur on the other side of the Atlantic. This is of course not so; and consequently, misdeterminations may result which are more troublesome than the possible synonyms which might occasionally result if such species were described as new.

Aside from these difficulties, the number of species completely known and ready to be inserted in any classification of the genus *Mycena* is comparatively large. This is due to the fact that two unusually industrious and ingenious monographers have studied the Mycenae of both Europe and North America, and some additional taxa could be added from South America, Northern Asia, and the Caucasus. Nevertheless, the species of *Mycena* from Southern and Eastern Asia, Australia, and Oceania, and to a lesser degree those from Africa, South and Central America have remained relatively poorly known.

It is desirable that now, after so much valuable work has been done in Europe and North America, a world monograph be written representing the actual knowledge on the *Mycenae*.

Below, the species known have been sifted twice. In the first place, only those known in every aspect are admitted, and in the second place, only those that do not cause any doubt as to their position have been chosen to illustrate the sections, subsections, and stirpes. This policy has reduced the species to 309, a figure which will steadily grow in accordance with further collecting and type studies mainly on species from regions where the *Mycena* flora has thus far not been sufficiently studied.

*Practical importance:* It is probable that Mycenae cause various plant diseases in the tropics but few details are available at present. The only definite knowledge we have, concerns *M. citricolor* which is pathogenic on *Coffea* (American Coffee Leaf Disease or Ojo de Gallo). Certain species have been indicated as edible or poisonous but they are of no economic importance. *M. pura* is said to cause poisoning of the muscarine type in Hungary (G. Makara, *Mikolog. Közlem.* 3: 139. 1972) which has been confirmed by the discovery of muscarine and epimuscarine in this species by Stadelman et al. (*Helv. Chem. Acta* 59: 2434. 1976); epimuscarine has also been found in another species of the same section: *M. pelianthina*.

## SPECIES

Sect. 1. *SACCHARIFERA* Kühner (1938). Species without basal disc or with basal disc; covering of the pileus not gelatinized, including a large number of inflated-vesiculose cells which are often acanthocyst-like and generally diverticulate, at times their walls thick or becoming swollen in KOH, often the individual cells separating and producing a pulverulent epithelium containing free cherocytes.

*Type species: M. tenerrima* (Berk.) Sacc.

*M. tenerrima* (Berk.) Sacc. (sensu Lange, Kühner); *M. osmundicola* Lange; *M. yalensis* Sing.; *M. copriniformis* Speg.; *M. mostnyae* Sing.; *M. biornata* Sing.; *M. trichocephala* Sing.; *M. amazonica* Sing.; *M. chloroxantha* Sing.; *M. araujae* Sing.; *M. asterophora* Sing.; *M. discogena* Sing.; *M. dryopteridis* Sing.; *M. nothomyrciae* Sing.; *M. sotae* Sing.; *M. triplotricha* Sing.

Sect. 2. *BASIPEDES* (Fr.) Kühner (1938). Stipe at the base with an abrupt broadening in form of a disc (formed by short, inflated, fusiform or ellipsoid hyphae); covering of the pileus typically including a distinctly gelatinous layer. Blue or blue-green pigments absent.

*Type species: M. stylobates* (Pers. ex Fr.) Kummer.

*M. stylobates* (Pers. ex Fr.) Kummer (sensu Schröter); *M. pseudostylotabes* Sing.; *M. mucor* (Batsch ex Fr.) Gillet (sensu Lange); *M. gaultheri* A.H. Smith; *M. clavularis* (Fr.) Sacc. (sensu Kühner); *M. bulbosa* (Cejp) Kühner; *M. longiseta* Höhn.

Sect. 3. *CYANOCEPHALAE* (Sing.) Sing.\* As sect. 2, but with blue to blue-green pigments when fresh. Species of the Southern Hemisphere.

*M. cyanocephala* Sing.; *M. veneta* Stevenson; *M. interrupta* (Berk.) Sacc. (the three species considered identical by Horak).

Sect. 4. *VISCIPELLES* Kühner (1931) (*Cyanescentes* Kühner 1938). Stipe not broadened into a basal disc, the base of the stipe blue, caesious green, stipe entirely pubescent under a lens; covering layer of the pileus gelatinous.

*Type species: M. cyanorhiza* Quél. (sensu Kühner).

*M. cyanipes* Godey ex Sing. (*M. cyanescens* Velen. non Mont.); *M. amicta* (Fr.) Quél. (sensu Höhn.) (*Prunulus caesioalbus* Murr.); *M. cyanorhiza* Quél. (sensu Kühner); *M. subcaerulea* (Peck) Sacc.; *M. caesiocana* Sing.; *M. cyanosyringea* Sing. in Sing. & Gomez; *M. limbata* (Lasch) Sacc. (type seen; may be too close to *M. amicta*); *M. pachyderma* Kühner.

Sect. 5. *CITRICOLORES* Sing. (1961). Stipe not broadened into a disc at the base which is subinsititious; epicutis of pileus simply and secondarily diverticulate; trama of pileus gelatinous, cheilocystidia of the dendrophysoid type; gelatinous hyphae inamyloid, non-gelatinous tissues strongly pseudoamyloid; habit omphalioid; spores ellipsoid to oblong, rather small, inamyloid. Asexual generation on living tree leaves where stilboids are formed. Neotropical: Guatemala to Bolivia.

*M. citricolor* (Berk. & Curt.) Sacc. (*Omphalia flava* Maublanc & Rangel; *Mycena*, Sing.; *Stilbum flavidum* Cooke; *Stilbella*, Kohl).

Sect. 6. *RADIATAE* Sing. (1961). Stipe not broadened into a disc at the base which is insititious, or subinsititious, without any blue pigment, pruinose to fibrillose-pubescent all over; epicutis of pileus with non-diverticulate long elements (hairs) or

\*Sect. nova. A sect. *Basipedes* pigmentis caesiis, caeruleis vel glaucis differt. Typus: *M. cyanocephala* Sing.

chains of short elements, etc.; basidia often remarkably short and broad; cheilocystidia often absent, if present not acanthophysoid, but sometimes hair-like; tramal hyphae with irregular and inconstant clamp connections; pileus plicate in the manner of the *Coprinini* or becoming rimose; lamellae free or subfree; habit mycenoid to mycenoid-pluteoid; spores amyloid, hyaline, ellipsoid to cylindric, thin-walled and without a germ pore; hyphae pseudoamyloid or not; generally on wood or woody humus; stilboids not known. Thermophilous: South America, Oceania, and Africa, probably widely distributed in the tropics.

Type species: *M. radiata* (Dennis) Sing.

*M. dennisii* Sing. (*Corrugaria alba* Dennis, non *Mycena alba* (Bres.) Kühner); *M. radiata* (Dennis) Sing. (*Corrugaria radiata* Dennis); *M. squamulosa* Sing. (*Leptomyces squamulosus* Mont.?); *M. chlorinosma* Sing.; *M. multicaudata* Sing.; *M. alosma* Sing. (probably only an inodorous variety of the following species); *M. umbilicata* Dennis; obviously also here or very closely related: *Corrugaria viridiflava* Métrod and probably *Mycena lenta* Maire, *Hiatula boninensis* Berk. & Curt. [recte *Mycena boninensis* (Berk. & Curt.) Sing.].

Note: This section is very remarkable within the genus. It is very probable that this is the original *Hiatula* Fr. and *Leptomyces* Mont. as well as *Leucoinocybe* Sing. (1943). The appearance of these species may suggest a certain affinity with the Agaricaceae but the spores are decidedly not of the type found in that family.

Sect. 7. *KERMESINAE* Sing.\* Stipe not broadened into a disc at the base which is subinsititious but base region pilose-hirsute; epicutis of pileus consisting of multi-appendiculate cylindrical to subvesiculose cells forming a subhymeniform layer above a ± epithelial hypodermium; no gelatinized layer in the cortical zone; lamellae adnate, with or without a discolored edge; tramal hyphae pseudoamyloid; spores ellipsoid, amyloid. Neotropical and Southern hemisphere species with bright colors (blue or red) fading to gray or yellow.

Type species: *M. kermesina* Sing.

*M. kermesina* Sing.\*\*; *M. eucryphiarum* Sing.

Sect. 8. *MYCENA*. (*Rigidipedes* and *Insititiae* Fr. sect. Agarici, 1836.) Pileus and stipe confluent, i.e. not separated by a separation layer as in the first four sections; stipe neither containing a latex nor covered with a glutinous sheath; pigment dull colored, or else pileus with an epicutis consisting of diverticulate hyphae (or hyphae at least nodose ramos), spores generally amyloid.

Type species: *M. galericulata* (Scop. ex Fr.) S.F. Gray.

Subsect. *Corticola* Kühner (1938). Small species on the cortex of living trees, more rarely of fallen branches, with pruinose, often insititious stipe, with mostly globose or subglobose to short ellipsoid spores. Cheilocystidia as in the following subsections.

\*sect. n. *Stipitis* basi hirsuta vel subinsititia; epicute subhymeniformi.

\*\*sp. n. *Characteribus* sectionis; pileo laetissime rubro. Typus Singer B 10252 (INPA).

*Type species: M. corticola* (Pers. ex Fr.) S.F. Gray sensu Pat. non Pers. (= *M. meliigena* (Berk. & Cooke) Sacc.).

*M. venustula* Quél.; *M. supina* (Fr.) Kummer (sensu Lange); *M. pseudocorticola* Kühner; *M. madronicola* A.H. Smith; *M. corticalis* A.H. Smith; *M. meliigena* (Berk. & Cooke) Sacc. (*M. corticola* (Pers. ex Fr.) S.F. Gray sensu Pat. non Pers.); *M. hypsizyga* Sing. (*Marasmius meliae* J.E. Wright); *M. melinocephala* Sing.; *M. costaricensis* Sing. in Sing. & Gomez; *M. abieticola* Sing.

Subsect. *Mycena* (Granulatae (Lange) Sing. 1951). Cheilocystidia of Lange's type II, i.e. usually vesiculose or vesiculose-pedicellate to clavate, rarely of some other shape, with short to long cylindric or rameous finger-like or rod-like appendages over the apical region or over most of their surface which gives them an echinate appearance, rarely cheilocystidia balloon-shaped and with 0-4 inconstant appendages only; pleurocystidia either absent, or like the cheilocystidia, or only the pleurocystidia warty to echinate on their ventricose middle portion or on their apical portion (stirps *Latifolia*).

*Type species: M. galericulata* (Scop. ex Fr.) S.F. Gray.

Stirps *Polyadelpha* (very small carpophores without rhizoids or with long mycelial filaments which radiate from the otherwise insititious base; edge of the lamellae rarely (and then stipe filamentous rising from leaves, fronds, or culms) differently colored).

*M. capillaris* (Schum. ex Fr.) Kummer (sensu Lange); *M. smithiana* Kühner; *M. tubarioides* (Maire) Kühner; *M. lohwagii* sing.; *M. herbarum* Sing.; *M. juncicola* (Fr.) Gillet (sensu A.H. Smith); *M. quercus-ilicis* Kühner; *M. polyadelpha* (Lasch) Kühner; *M. pterigena* (Fr.) Kummer; *M. typhae* (Schweers) Kotlaba.

Stirps *Elegans* (edge of the lamellae discolored because of a dissolved pigment in the cheilocystidia, or else pileus brightly pigmented but then epicutis consisting of distinctly diverticulate hyphae and spores strongly amyloid; stipe > 1 mm broad, on needle beds, more rarely on wood, mostly temperate.)

*M. aurantiomarginata* (Fr.) Quél. sensu Schroeter [*M. elegans* (Pers. ex Fr.) Kummer sensu Kühner]; *M. chlorantha* (Fr. ex Fr.) Kummer sensu Oort [*M. elegans* (Pers. ex Fr.) Kummer sensu Smith]; *M. flavescens* Vel.; *M. luteolorufescens* Karst.; *M. strobilinoides* Peck; *M. piguicola* Sing.; probably also *M. beardsleeana* Sing.

Stirps *Rosella* (edge darker colored than the sides of the lamellae; the latter with smooth fusoid-ampullaceous cystidia).

*M. rosella* [(Fr.) Kummer sensu Schroeter, and (if identical) sensu A.H. Smith].

Stirps *Monticola* (pileus often brightly colored; spores extremely weakly amyloid; epicutis consisting of nodose and somewhat rameous filamentous hyphae; lamellae with concolorous edge).

*M. monticola* A.H. Smith; perhaps also *M. subincarnata* (Peck) Sacc.

Stirps *Galericulata* (pileus usually not bright colored, or if bright colored, not combining the characters of either *stirps elegans* or *stirps monticola*).

*M. piceicola* A.H. Smith; *M. plicosa* (Fr.) Kummer sensu Smith; *M. subplicosa* Karst. sensu Smith; *M. kuehneri* Sing.; *M. amygdalina* (Pers.) Sing. [Agaricus, Pers.; *M. vitilis* (Fr.) Quél. sensu Kühner vix Fr.; *M. iodiolens* Lundell]; *M. phyllogena* (Pers.) Sing. [*M. vitrea* var. *tenella* (Schum. ex Fr.) Kühn. sensu Kühner]; *M. urania* (Fr.) Quél. sensu Smith; *M. alexandri* Sing. [*M. psammicola* (Berk. & Br.) Sacc. sensu A.H. Smith non (Berk. & Br.)]; *M. peyerimhoffii* R. Maire; *M. xantholeuca* Kühner; *M. pusilla* A.H. Smith; *M. alcaliniformis* (Murr.) Murr.; *M. atroalboides* (Peck) Sacc.; *M. rugosa* (Fr.) Quél.\* (*M. rugulosiceps* (Kauffm.) A.H. Smith); *M. galericulata* (Scop. ex Fr.) S.F. Gray (*M. atkinsonii* House; *M. atridisca* Murr.); *M. hemisphaerica* Peck; *M. dissimilabilis* (Britz.) Sacc. (*M. megaspora* Kauffm.; *M. excisa* (Lasch) Kummer sensu Bres. non al.; *M. permixta* (Britz.) Sacc. sensu Sing., Moser nec Stangl & Bresinsky); *M. occidentalis* (Murr.) Murr.; *M. albogrisea* Peck (*M. filopes* sensu A.H. Smith); *M. turficola* Sing.; *M. mirata* (Peck) Sacc.; *M. minutuliaffinis* Sing.; *M. maculata* Karst. [*M. alcalina* (Fr.) Kummer sensu Ricken; *M. parabolica* (Fr.) Quél. sensu Bres.; *M. rugosoides* Peck]; *M. tintinnabulum* (Fr.) Qél. sensu Schroeter; *M. inclinata* (Fr.) Quél. sensu Kühner; *M. radicatella* (Peck) Sacc. (*Prunulus adirondackensis* Murr.; *M. subviscida* Kauffm. & Smith); *M. longipes* (Murr.) Murr. (*Prunulus magnus* Murr.).

Stirps *Cinerella* (differs from the preceding stirps in having a very distinct omphalioid habit, horizontal, arcuate-decurrent lamellae, and relatively less thin stipe; pigment always dull colored (gray or fuscous), or (rarely) absent.

*M. cinerella* Karst. (sensu Lange); *M. subconcolor* A.H. Smith; *M. concolor* (Lange) Kühner; *M. omphalophora* Sing.; *M. papilligera* Sing.; *M. microxantha* Sing.

Stirps *Latifolia* (differs from the preceding stirps in having pleurocystidia which are projecting, fusoid like those of the *Cliliatae* but acanthophysoid-echinate in the middle portion; habit mycenoid to omphalioid.).

*M. latifolia* (Peck) Sacc. (*M. pinetorum* Lange); *M. fontqueri* Maire.

Stirps *Borealis* (differs from the preceding stirps in having the diverticulation at the apex of hyphous or fusoid cheilocystidia; similar or non-diverticulate pleurocystidia more or less differentiated; trama of the pileus weakly pseudoamyloid or almost inamyloid).

*M. borealis* A.H. Smith; *M. februaria* Sing.

Stirps *Juanicola* (Cheilocystidia balloon-shaped, either entire or with few apical appendages ("Siccus-type") or with short ventricose main body and one very long filiform appendage; spores often weakly (but undoubtedly) amyloid; trama pseudo-

\*This species, always (2)-4-spored, without farinaceous odor, with the lamellae usually not becoming evenly flesh-pink, is the *M. rugosa* of the Czechoslovakian mycologists.

amyloid or not; lamellae adnate or decurrent, pileus and/or stipe often long-hyaline-pilose).

*M.juanicola* Sing.; *M. dinae* Sing.; *M. cyanella* Sing.; *M. heterotrama* Sing.; *M. microtrichialis* Sing.; *M. hyalinotricha* Sing.; *M. desfontaineae* Sing. in Sing. & Moser.

Stirps *Helminthobasis* (differs from the corresponding stirps - *Omnium-sanctorum* - of the following subsection only by the echinate-appendiculate cheilocystidia; there is a gelatinized epicutis and a gelatinized infrahypodermial zone in the pileus.).

*M. helminthobasis* Sing.

Subsection *Ciliatae* (Lange p.p. 1914) Kühner (1938). Pleurocystidia either absent or not echinate but smooth; cheilocystidia always smooth and not appendiculate and vesiculose at the same time but, if elongated (fusoid, ampullaceous etc.) either entire or with a few large branches, or finger-like appendages.

Type species: *M. alcalina* (Fr.) Kummer (sensu Schroeter).

Stirps *Brownii* (with the same characters as stirps *Cinerella* of subsection *Granulatae* but differing in cystidial characters; trama of the pileus sometimes inamyloid; pileus sometimes viscid; pigments often entirely absent; stipe rarely somewhat eccentric; lamellae rarely nearly absent).

*M. brownii* A.H. Smith; *M. pseudoclavicularis* A.H. Smith; *M. austrocapillaris* Sing.; *M. cuticolor* (Murr.) Sing.; *M. rubrimontana* Sing.

Stirps *Carminis* (with the same characters as the preceding stirps, but with bright pigments in the pileus; reminiscent of sect. *Adonideae*).

*M. carminis* Sing.; *M. chusqueophila* Sing. in Sing. & Moser; *M. nothofagetorum* Sing.; *M. xanthocephala* Sing.; *M. mesospora* (Sing.) Sing.

Stirps *Rubromarginata* (with the same characters as stirps *Elegans*, but with different cystidial characters; habit mycenoid).

*M. capillaripes* Peck (*M. langei* Maire); *M. debilis* (Fr.) Quél. (sensu A.H. Smith); *M. citrinomarginata* Gillet; *M. cedretorum* Maire; *M. avenacea* (Fr.) Quél. (sensu Schroeter, Kühner); *M. thymicola* Velen.; *M. albidolilacea* Kühner & Maire; *M. viridimarginata* Karst.; *M. olivaceoalcalina* Sing.; *M. atromarginata* (Lasch) Kummer; *M. fernandeziana* Sing.; *M. rubromarginata* (Fr.) Kummer; *M. endoglobulosa* Sing.; *M. elegantula* Peck; *M. purpureofusca* Peck; *M. luteoalcalina* Sing.; *M. renati* Quél.; *M. seynii* Quél.; *M. rhaeborhiza* (Lasch) Kummer (*M. lutea* Bres.); *M. chrysocorypha* Sing.; *M. olivaceobrunnea* A.H. Smith.

Stirps *Palmivora* (pileus partly bright colored and beset with numerous small, filiform, rarely somewhat ampullaceous dermatocystidia; these forming a turf above the hypodermium, rather than a cutis-like epicutis; spores amyloid; trama pseudoamyloid; habit almost collybioid, much like *Marasmius* sect. *Globulares*).

*M. palmivora* Sing.; *M. oreadeoides* Sing.

Stirps Alcalina (with the characters of stirps Galericulata, but cystidia elongated and not as in stirps Juaniicola; habit mycenoid).

*M. zephyrus* (Fr. ex Fr.) Kummer; *M. strobilicola* Favre & Kühner (*M. vernalis* Post ex Lundell non Velen.); *M. alcalina* (Fr.) Kummer (sensu Schröter, Kühner); *M. chlorinella* (Lange) Sing. (*M. alcalina* var. *chlorinella* Lange); *M. metata* (Fr.) Kummer sensu Schröter; *M. leptocephala* (Pers. ex Fr.) Gillet sensu Ricken - both vix sensu Fires); *M. debiliformis* Sing.; *M. saxegotheae* Sing.; *M. munyozi* Sing.; *M. macrocystidiata* Sing.; *M. atrocyanea* (Batsch ex Fr.) Gillet (sensu Kühner) (*M. nigricans* Bres.); *M. blechnophila* Sing. in Sing. & Moser; *M. microleuca* Sing. in Sing. & Moser; *M. patagonica* Sing.; *M. fragillima* A.H. Smith; *M. plumbea* (Fr.) Karst.; *M. subvitrea* A.H. Smith; *M. griseoconica* Kauffm.; *M. praecox* Velen.; *M. niveipes* (Murr.) Murr. (*M. pseudogaleruculata* Lange; *M. jacobi* Kühner); *M. atroalba* (Bolt. ex Fr.) S.F. Gray (sensu Ricken); *M. adalberti* Sing. (*M. vitilis* (Fr.) Quél. sensu Bres. non al.); *M. tenuiceps* A.H. Smith; *M. josephi* Sing. (ined. - *M. atroalba* (Bolt. ex Fr.) S.F. Gray sensu Velen.); *M. excisa* (Lasch) Gillet (sensu Kühner); *M. sudorella* Sing.; *M. fagetorum* (Fr.) Gillet; *M. pseudoalnicola* Sing.; *M. paraboliciformis* Sing. (*M. parabolica* (Fr.) Quél. ss. Smith); *M. rosaceifolia* Sing.; *M. rhizogea* (Pers.) Sing.; *M. polygramma* (Bull. ex Fr.) S.F. Gray (sensu Lange); *M. vitilis* (Fr.) Quél. sensu Lange (*M. filopus* (Bull. ex Fr.) Kummer sensu Schröter; *M. adhaerens* Velen.); *M. pullata* (Berk. & Cooke) Sacc. (sensu A.H. Smith; *M. kauffmaniana* A.H. Smith; *M. subfuscata* A.H. Smith; *M. murina* (Murr.) Murr.; *M. stannea* (Fr.) Quél. sensu A.H. Smith; *M. pectinata* (Murr.) Murr.; *M. praelonga* (Peck) Sacc.; *M. subsupina* A.H. Smith; *M. rubrotincta* A.H. Smith [*M. tenuicula* (Murr.) Murr. non (Karst.) Sacc.]; *M. tetrasphaerophora* Sing.; *M. humilis* Rick; *M. pratensis* Sing.; *M. atroincrustata* Sing.; perhaps here *M. fimetaria* (Murr.) Sing. (cystidial characters unknown).

Stirps Metuloidifera (like the preceding stirps but with metuloids) *M. metuloidifera* Sing.; *M. cystidiosa* (Stevenson) Horak (*Fayodia*, Stevenson).

Stirps Austroalcalina (like stirps Alcalina but spores not appreciably amyloid) *M. austroalcalina* Sing.; *M. valdiviana* Sing.

Stirps Omniumsanctorum (differs from stirps Alcalina by the broad ixocutis of the pileus).

*M. omniumsanctorum* Sing.; *M. algeriensis* Maire apud Kühner with var. *hypoxera* Sing. and var. *peraffinis* Sing.; *M. laevigata* (Lasch) Quél.

Sect. 9. LACTIPEDES Fr. ut sect. gen. *Agarici* trib. *Mycenae* (1836). Stipe with laticifers containing white or colored milky or latex (latex watery, sometimes inconspicuous); stipe and pileus not viscid).

Type species: *M. galopoda* (Pers. ex Fr.) Kummer.

Subsection *Galactopodinae* (Earle) Sing. (st. n.: *Galactopus* Earle, ut genus, *Bull.*

*N.Y. Bot. Gard.* 5: 426. 1909, em.). Cystidia entire or forked, or only pseudo-cystidia present; latex white, red, or absent to aqueous.

Type species: *Agaricus haematopus* Pers.

Stirps *Galopoda* (latex white; taste mild).

*M. galopoda* (Pers. ex Fr.) Kummer; apparently also *M. cayugaensis* A.H. Smith; possibly (cystidia not found in the type) *M. obtusiceps* Speg.

Stirps *Haematopoda* (latex red, purple, orange, blue(?) etc.)

*M. haematopoda* (Pers. ex Fr.) Kummer; *M. atkinsoniana* A.H. Smith; *M. sanguinolenta* (A. & S. ex Fr.) Kummer; *M. subsanguinolenta* A.H. Smith; *M. poecila* Sing.

Stirps *Erubescens* (latex white or absent; carpophores often tending to redden; pseudocystidia filled with coarse or fine granules, numerous; taste bitter in the type, unknown in other species.)

*M. erubescens* Höhn.; *H. delica* Sing.

Subsection *Pseudocrocatae* Sing.\*. Latex colored, or absent; cheilocystidia and cystidia (if present) with setulae or thorns.

Type species: *M. pseudocrocata* Dennis.

*M. pseudocrocata* Dennis; *M. crocata* (Fr.) Gillet sensu Singer 1929, Kühner 1938; *M. melandeta* Sing.

Sect. 10. *HYGROCYBOIDEAE* (Fr.) Sing. (1972) (*Agaricus* trib. *Mycena* sect. *Glutinipedes* Fr. 1838; *Gummosae* Lange 1914; *Glutinosae* Kühner 1931). Stipe in cross section showing an outer gelatinous layer, hence usually viscid when fresh, or showing a glutinous sheath.

Type species: *M. epiphytigia* (Scop. ex Fr.) S.F. Gray.

Subsect. *Fuliginellae* A.H. Smith ut sectio (1947). Pileus not with a corticate layer consisting of broad inflated cells (some with brown contents); stipe not yellow or otherwise bright colored. Mycelium humicolous; carpophores not cespitose (but often densely gregarious).

Type species: *M. vulgaris* (Pers. ex Fr.) Kummer.

*M. insignis* A.H. Smith; *M. clavicularis* (Fr.) Gillet; *M. militaris* Karst.; *M. vulgaris* (Pers. ex Fr.) Kummer; *M. pelliculosa* (Fr.) Quél.; *M. odorifera* (Peck) Sacc.; *M. quinaultensis* Kauffm. apud A.H. Smith; *M. tenax* A.H. Smith; *M. mackinawensis* A.H. Smith; *M. idroboi* Sing.; *M. pseudovulgaris* Kühn.

Subsect. *Gummosae* (Lange) Oort (1928) (sect. *Viscosae* Smith 1947). Pileus without a corticate layer consisting of broad, inflated cells (some with brown contents); stipe-base or pileus olive or yellow or otherwise bright colored.

\*sect. n. Cheilocystidiis diverticulatis vel multispinulosus.

Mycelium humicolous (or on very old decayed wood); carpophores as a rule not cespitose.

Type species: *M. epipterygia* (Scop. ex Fr.) S.F. Gray.

*M. griseoviridis* A.H. Smith; *M. subinamyloidea* Sing.; *M. ixoxantha* Sing.; *M. leucoxantha* Sing.; *M. subulifera* Sing.; *M. piterbargii* Sing.; *M. viscosa* (Secr. ex) Maire (*Agaricus alcalinus viscosus* Secr.; *M. epipterygia* var. *viscosa* Ricken); *M. epipterygioides* Pearson; *M. epipterygia* (Scop. ex Fr.) S.F. Gray (*Prunulus paludicola* Murr.); *M. citrinella* (Pers. ex Fr.) Quél. (unless too close to the preceding species).

Subsect. *Caespitosae* A.H. Smith ut sectio (1947). Pileus not with a corticate layer consisting of broad inflated cells (some with brown contents); stipe either orange to yellow, or dull colored to white; mycelium lignicolous; carpophores as a rule fasciculate-cespitoso, rarely gregarious.

Type species: *M. texensis* A.H. Smith.

*M. glutinosa* Beardslee; *M. subglutinosa* Sing.; *M. austini* (Peck) Kühner; *M. hondurensis* A.H. Smith; *M. texensis* A.H. Smith; *M. leaiana* (Berk.) Sacc.; *M. roriduliformis* (Murr.) Dennis (?*M. roridula* (Berk. & Curt.) Sacc.); *M. euspeirea* (Berk. & Curt.) Sacc.; *M. muciflua* (Höhn.) Sing. (*Collybia*, Höhnel); *M. micromphale* Sing.

Subsection *Lilacifolinae* Sing.\*. Differs from the preceding subsections in inamyloid spores; cheilocystidia often absent, or at least not crowded.

Type species: *M. lilacifolia* (Peck) A.H. Smith.

*M. lilacifolia* (Peck) A.H. Smith; obviously also *Omphalina cyanophylla* (Fr.) Quél. (unless too close to the preceding species) and *Gerronema glutinipes* Pegler.

Sect. 11. *RORIDAE* Kühn. (1931). Pileus with a corticate, ± hymeniform layer of broad, inflated cells, some of them often with brown contents (vacuolar pigment); stipe glutinous. Gregarious, lignicolous or not.

Type species: *M. rorida* (Scop. ex Fr.) Quél.

*M. rorida* (Scop. ex Fr.) Quél.; *M. austrororida* Sing.; according to Horak (1978) also *M. lamprospora* (Corner) Horak, *M. praecleara* Horak; *M. irritans* Horak.

Sect. 12. *PURAE* Konr. & Maubl. (1924-37) (*Ianthinae* Kühner, as A.H. Smith ut subsectio 1947). Pigment rarely dull colored often violet or rose color etc.; cuticle consisting of a poorly developed hypodermium and an equally poorly developed epicutis, the latter consisting of smooth hyphae; trama pseudoamyloid and spores amyloid or spores inamyloid but hyphae pseudoamyloid; carpophores usually rather fleshy with raphanaceous odor, collybioid, clitocyboid, or tricholomatoid rather than mycenoid in some cases; lamellae often intervenose.

Type species: *M. pura* (Pers. ex Fr.) Kummer.

\*subsect. n. Sporis inamyloideis.

Stirps *Pelianthina* (edge of the lamellae darker colored; spores amyloid).

*M. pelianthina* (Fr.) Quél.; *M. rutilantiformis* (Murr.) Murr. (*Prunulus*, Murr.; *M. pseudopelianthina* Lange); *M. austroavenacea* Sing.

Stirps *Pura* (edge of the lamellae concolorous with the sides; spores amyloid).

*M. pura* (Pers. ex Fr.) Kummer; *M. kuehneriana* A.H. Smith; *M. subaquosa* A.H. Smith; *M. holoporphrya* (Berk. & Curt.) Sing. (*Clitocybe* Sacc.); *M. griseirete* Sing.; *Phlebomycena madagassensis* Heim obviously belongs here according to description by Heim.

Stirps *Violacella* (lamellae often strongly anastomosing and spores always inamyloid).

*M. pearsoniana* Dennis ex Sing.; *M. viridula* (Berk. & Cooke) Sing. (*Laschia*, Cooke); *M. violacella* (Speg.) Sing. (*Heliomyces*, Speg.; *Collybia*, Speg.; *Poromycena anastomosans* Sing.); *M. sosarum* Sing.; obviously also *M. decipiens* Van Overeem in Van Overeem & Weese (unless to stirps *Pura*).

Sect. 13. *ADONIDEAE* (Fr. 1836 ut sectio *Agarici, Mycena*) Sing. (1943 ut sect. *Hemimycenae*). Habit mycenoid to almost omphaloid (rarely) with soft (neither tough nor fragile) stipe which is confluent with the pileus; lamellae ascendant at first, rather narrow; pigment bright colored (red, orange, pink, yellow) or rarely none at all; (pleuro- and cheilo-)cystidia present; cystidia with narrow tip; hymenophoral trama regular to intermixed; epicutis consisting of diverticulate hyphae; conducting elements (laticiferous hyphae?) usually abundant.

Type species: *M. adonis* (Bull. ex Fr.) S.F. Gray.

*M. flavoalba* (Fr.) Quél.; *M. floridula* (Fr.) Karst. (*Collybia*, Ricken); *M. adonis* (Bull. ex Fr.) Kummer; *M. rubella* Quél.; *M. ribesina* Sing.; *M. heroica* Sing.; perhaps also *Mycena roseocandida* (Peck) Sacc., *Prunulus fusipes* Murr., and *Prunulus aurantiidiscus* Murr.

Sect. 14. *ACICULAE* (Kühn.) Sing. Habit mycenoid, with soft, central, concolorous stipe which is distinct from the pileus (separated by a zone with small elements); lamellae initially more or less ascendant, adnate, or with descendant tooth, not ventricose; pigment microscopically yellow, macroscopically orange or red; cheilocystidia and (mostly) also (pleuro-)cystidia present; trama subregular; epicutis of the pileus consisting of diverticulate hyphae; conducting elements none, or very few.

Type species: *M. acicula* (Schaeff. ex Fr.) Kummer.

*M. acicula* (Schaeff. ex Fr.) Kummer; probably also *M. oregonensis* A.H. Smith (*M. siskyouensis* A.H. Smith), inserted here by Kühner, *M. xanthopoda* (Dennis) Sing.; *M. coccinea* (Murr.) Sing. (*Omphalina*, Murr.; *Agaricus sanguineus* Berk. & Curt. non Wulf ex Fr.), and *M. aequatorialis* Sing.

Sect. 15. *HIEMALES* Konr. & Maubl. (1924-38).

Habit mycenoid or almost omphaloid, with soft but not always fragile stipe which

is more or less separated from the tissue of the pileus by a differentiated tissue-zone as in sect. *Aciculae*; lamellae ascendant, or horizontal at first, subfree to decurrent; pigment dusky, dull (gray, fuscous, melleous, blackish), rarely orange to pink or lacking (and then the stipe white at the apex in young specimens); (pleuro-)cystidia often present; cheilocystidia always present, not diverticulate\*; epicutis consisting of diverticulate or (rarely) non-diverticulate hyphae; conducting elements none or very few; spores inamyloid; hyphae subinamyloid or pseudoamyloid in the stipe, inamyloid or almost so in the pileus.

*Type species:* *M. hiemalis* (Osb. in Retz ex Fr. sensu Gillet) Quél.

Subsect. *Typicae* Kühn. (1938). Lamellae strongly ascendant when young. Probably merely a stirps.

*Type species:* As in the section.

*M. roseipallens* (Murr. sensu A.H. Smith) Sing. (*Prunulus*, Murr.); *M. leptophylla* (Peck) Sacc.; *M. olida* Bres.; *M. americana* (A.H. Smith) Sing.; *M. hiemalis* (Osb. in Retz ex Fr. sensu Gillet); *M. corticola* (Pers. ex Fr.) Gray (ss. Pers., Bres., Quél.), the latter being intermediate between *Typicae* and *Omphaliariae*.

Subsect. *Omphaliariae* Kühn. (1938). Lamellae not strongly ascendant at first. Probably merely a stirps.

*Type species:* *Mycena speirea* (Fr. ex Fr.) Gillet sensu Kühner (non Fr.).

*M. camptophylla* (Berk.) Sing. [*Omphalia*, Sacc.; *Mycena speirea* (Fr. ex Fr.) Gillet sensu Kühner (non Fr.), nec Hoehnel; *Omphalia*, Cepl]; *M. atropapillata* Kühner & Maire; *M. phaeophylla* Kühn.; *M. drepanocladii* (Sing.) Sing. (*Hemimycena*, Sing. 1943); *M. foliicola* (Sing. in Sing. & Digilio) Sing.; *M. subtropicalis* Sing.; *M. alba* (Bres.) Kühner (*Omphalia*, Bres.).

Subsect. *Insititiopedes* Sing. (1961). Differs from the two preceding groups of this section in ± insititious stipe.

*Type species:* *M. tucumanensis* Sing.

*M. tucumanensis* Sing.; *M. neospeirea* Sing.; *M. petiolorum* (Berk. & Curtis) Dennis.

## 99. HYDROPOUS (Kühn.) Sing. ex Sing.

*Lloydia* 5: 129. 1942, *nom. subnud.*; *Pap. Mich. Acad. Sc. Arts & Lett.* 32: 127. 1946 (publ. 1948).

*Type species:* *H. fuliginarius* (Batsch ex Fr.) Sing. sensu Kühner (1938), Singer (1948) (= *H. nigrita*).

Syn.: *Mycena* subgen. *Eu-Mycena*, group Spuriae 3° (section?) *Hydropus* Kühner, *Le Genre Mycena*, p. 531. 1938, *nom. nud.*

*Caulorhiza* Lennox, *Mycotaxon* 9: 154. 1979.

\*Species with diverticulated cheilocystidia ("Rotalis type" or similar) are here considered as belonging in *Hemimycena* which should be compared.

**Characters:** Habit between mycenoid and collybioid, or much more frequently omphaliod or between omphaliod and clitocyboid, rarely pleurotoid (with somewhat eccentric stipe); epicutis of the pileus consisting of fascicles of generally non-continuous subhymeniformly organized elements which are broad, usually ventricose, even vesiculose, always rounded above, frequently pigmented (pigment generally intracellular and dissolved, mostly fuscous-gray, fuscous, pale fuscous, tan, rarely negropigments incrusting, sometimes easily collapsing, sometimes isolated, in one section (*Floccipedes*) rare and inconspicuous or entirely replaced by a cutis of very thin-filamentous appressed hyphae which are often pigmented by a dissolved intracellular pigment, or else hyaline (if broad erect elements are absent - stipe often scabrous and pleurocystidia conspicuous); stipe often with a similar covering layer, never viscid; lamellae mostly adnate or decurrent, well developed, more rarely adnexed to free; hymenophoral trama regular, often strictly regular with parallel hyphae, not gelatinized except in a few species with gelatinized lateral and non-gelatinized mediostratum, never bilateral (except in primordia); trama of the carpophores monomitic, often with numerous strongly inflated and at the same time very long cells, intermixed ("sacro dimitic", weakly pseudoamyloid or much more frequently inamyloid, with clamp connections, rarely without clamp connections; conducting elements (oleiferous or laticiferous hyphae) often present, especially in the section *Hydropus*), context sometimes blackening; latex, if present, aqueous; basidia normal; basidioles not fusoid; spore print white; spores with thin, homogenous, hyaline, inamyloid or amyloid, acyanophilic wall; pleuro- and/or pseudocystidia or metuloids often present; cheilocystidia mostly present and often conspicuous; veil generally none or if present, silky and fugacious. On wood, humus, among mosses, on débris (Pl. 58, 1; 79).

**Development of the carpophores:** Gymnocarpous in most but apparently monovelangiocarpous in some species (e.g. *H. omphaliniformis*).

**Area:** Nearly cosmopolitan but majority of species subtropical and tropical.

**Limits:** The species with dermatocystidioid, large, rounded epicuticular bodies (section *Hydropus* and *Mycenoides*) differ from *Mycena* constantly in this very character. Only *Mycena* sect. *Roridae* has similar cells on the pileus, but they form a hymeniform layer and the stipe is covered by a glutinous sheath. In the sections with a hyphal cutis or ixocutis (sect. *Floccipedes*) where the habit is often almost collybioid, the distinction is less immediate, but the affinity with *Hydropus* can easily be established by either the presence of a scabrous stipe and small repent to ascendant dermatocystidioid clavate bodies, scattered as terminal cells of the epicutal hyphae, or by amyloid spores accompanied by almost or quite inamyloid tramal hyphae. The species with inamyloid spores and hyphae (subsection *Floccipedes*) are obviously quite distinct and not related to the corresponding sections of *Mycena* (*Aciculares* and *Hiemales*) because of their habit and tramal structure and the constantly smooth epicutis hyphae.

*Dermoloma*, although undoubtedly closely related to *Hydropus*, can be distinguished by the continuous hymeniform covering of the pileus combined with

an absence of cystidia and cheilocystidia, broad, deeply sinuate lamellae, and intraparietal and incrusting pigments.

Pigment topography is obviously important in the delimitation of *Hydropus*. The pigmented species of this genus have mostly vacuolar pigment, at any rate no distinct intraparietal or incrusting pigment except in a few species where these pigments are weak, only thinly incrusting or rather pale in the hyphal wall. These species were enumerated in *Flora Neotropica* 32: 9. 1982 but some of them are suspected to have only necro-pigments of this kind. On the other hand, fresh or freshly dried material of *Hydropus trichodermus* shows abundant dark incrusting and intraparietal pigment, and so, apparently, does *Hydropus ardesiacus*. Both species were considered to be congeneric with *Hydropus* (1975, 1982), but I believe now that they are better placed in *Dennisiomyces* because they are the only exceptions to an otherwise consistent generic characteristic of *Hydropus* and fit the generic description of *Dennisiomyces* in all important points.

Some species of *Clitocybula* are much like *Hydropus* sect. *Hydropus*. However, where dermatocystidia are developed, they exist in *Clitocybula* only in the center region of the pileus. The species of *Hydropus* sect. *Hydropus* coming close to *Clitocybula* sect. *Clitocybula* have more broad, very long hyphae characteristic for most *Hydropus* species, and are tropical rather than temperate elements.

Some species of *Gerronema* are comparable with certain species of section *Mycenoides* and may come close to some of *Floccipedes* subsection *Floccipedes*. A careful study of the structure of the epicutis and the hyphal structure in the trama will avoid misdeterminations, even in cases where there is a remarkable similarity in habit and colors (for example *Gerronema* sect. *Icterina*). Yet if we apply the same criteria here as in *Hydropus* versus *Clitocybula*, the distinctness of these genera is quite apparent.

There can be no doubt but that the similarity between *Clitocybula* and *Gerronema* with certain species of *Hydropus* is not coincidental but expresses affinity. This will easily be understood if, as we may assume, *Hydropus* derives from forms ancestral to Leucopaxilleae and Omphalinae (and thus from groups with generally simpler structure).

*Pseudohiatula* differs from all species of *Hydropus* in the distinctly bilateral hymenophoral trama. Thus, those species described originally in *Pseudohiatula* but with regular structure in both mediostratum and (the usually gelatinized) lateral stratum had to be transferred to *Hydropus* and those species, once inserted in *Hydropus*, like *H. irrorata* had to be transferred to *Pseudohiatula*. An additional sharp distinction between those two genera is seen in the continuously hymeniform epicutis with often dimorphic elements characteristic for *Pseudohiatula*.

There is also a group of *Marasmius* species belonging in section *Alliacei* where the pigment is exclusively vacuolar. For this reason they were at first thought to belong in *Hydropus* but they differ from *Hydropus* in a continuous hymeniform epicutis, and their basidioles tend to be fusoid.

As for *Tricholomopsis*, see there.

*State of knowledge:* Since most of the species of *Hydropus* are either tropical or south-temperate, the genus was at first believed to be a relatively small one, and became better known only after they had been studied in Southern South America (Singer, *Beih. z. Nova Hedw.* 29: 140-145, 1969), in Malaya as "Trogia" (Corner, *A. Monograph of Cantharellloid Fungi*, pp 175-244. 1963), and in a neotropical monograph devoted to this genus (*Flora Neotropica*, Mon. 32, 1982). The total number of species here admitted is 104. For illustrations see also *Nov. Hedw.* 35: 154, plate III.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *HYDROPOUS*. Epicutis with broad, inflated elements, with, more rarely without pigment; pigment mostly intracellular, vacuolar, rarely, in addition, some incrusting pigment on the epicuticular elements, these either singly or in fascicles or forming an interrupted hymeniform or subhymeniform layer, rarely forming a continuous hymeniform layer and then accompanied by thick-walled dermatocystidia which occur likewise on the surface of the stipe; otherwise stipe with or without dermatocystidia; spores always weakly (but distinctly) to strongly amyloid; trama of the pileus varying between weakly pseudoamyloid to inamyloid; carpophores often blackening, but also unchanging, if blackening, oleiferous or laticiferous hyphae numerous; clamp connections generally present; pellicle not gelatinous.

*Type species:* *H. fuliginarius* (Batsch ex Weinmann) Sing. (sensu Bres., Kühn., Sing.).

Subsection *Hydropus*. (Nigritae Sing. (1982) Blackening. - Type as in sect. 1.

*H. nigrita* (Berk. & Curt.) Sing. (*Collybia*, Sacc.; *Agaricus plexipes* b. *fuliginarius* (Batsch ex) Weinm. sensu Bres. non Batsch nec Weinm.; *A. fuliginarius* (Weinm.) Fr. ss. aut. non Weinm. nec Fr.; *Hydropus* Sing. non Batsch nec Weinm.); *H. beniensis* Sing.; *H. tucumanus* Sing.; *H. riograndensis* Sing.; apparently also *H. odoratus* Pegler & Rayner.

Subsection *Marginelli* Sing. (1982). Not blackening.

*Type species:* *H. marginellus* (Pers. ex Fr.) Sing.

*H. translucens* (Murr.) Sing.; *H. sabalis* Sing.; *H. chlorinodorus* Sing.; *H. grevilleae* Sing.; *H. fraterniger* Sing.; *H. praedecurrents* (Murr.) Redhead in litt. (*Mycena*, Murr., *Omphaliopsis*, Murr.); *H. subcartilagineus* (Murr.) Sing. with several varieties; *H. caespitosus* Sing.; *H. sinensis* Sing. ined.; *H. swaneticus* (Sing.) Sing.; *H. fluvialis* Sing. with var. *aporus* Sing.; *H. lutescentipes* Sing.; *H. veraecrucis* Sing.; *H. semimarginellus* Sing.; *H. marginellus* (Pers. ex Fr.) Sing.; *H. microsporus* Sing.; *H. atropruinosis* (Corner) Sing.; *H. atriceps* (Murr.) Sing.; *H. omphaliniformis* Sing.; *H. xerophilus* Sing.; *H. camarágibensis* Sing.; *H. nanus* Sing.; *H. cavipes* (Pat. & Gaillard) Dennis; *H. erinensis* (Dennis) Sing.; *H. umbo-*

*natus* (Peck) Sing. (*Caulorhiza*, *Lennox*); *H. brunnescens* (Murr.) Sing.; *H. excentricus* Sing.; *H. serifluus* (Murr.) Sing.; *H. confertifolius* Sing.; *H. xuthophylloides* Sing.; *H. dusenii* (Bres.) Sing. with subsp. *dusenii* and ssp. *nivifugus* Sing.; *H. africanus* Sing.; probably *H. paradoxus* Moser, *H. hymenocephalus* (A.H. Smith) Redhead, and *Mycena macilenta* Bigelow.

Sect. 2. *MYCENOIDES* Sing. (1961). Same characteristics as sect. 1, but spores inamyloid.

Type species: *H. mycenoides* (Dennis) Sing.

Subsection *Anthidepades* Sing. (1982). Cystidia present or absent; pseudocystidia and metuloids absent.

Type species: *H. anthidepas* (Berk. & Br.) Sing.

*H. dubius* Sing.; *H. cylindrisporus* (Dennis) Sing.; *H. angustispermus* Sing.; *H. nigromarginatus* Sing.; *H. amazonicus* Sing.; *H. platensis* Sing.; *H. albopubescens* Sing.; *H. hypopolius* Sing.; *H. subspodoides* (Murr.) Sing.; *H. aristoteliae* (Sing.) Sing.; *H. fragilior* Sing.; *H. chiriquiensis* Sing.; *H. glabripes* Sing.; *H. platycystis* Sing.; *H. pinetorum* Sing.; *H. rionegrensis* Sing.; *H. hydrophoroides* Sing.; *H. levius* Sing.; *H. dissiliens* Sing.; *H. altus* Sing.; *H. hyperythrus* Sing.; *H. brunneobasis* Sing.; *H. papillatus* Sing.; *H. stenocystis* Sing.; *H. lacuster* Sing. with var. *riparius* Sing.; *H. microcephalus* Sing.; *H. fimbriatus* Sing.; *H. maculatipes* Sing.; *H. humilior* Sing.; *H. megalobasidium* Sing.; *H. xuchilensis* (Murr.) Sing.; *H. anthrocophilus* (Dennis) Dennis; *H. anthidepas* (Berk. & Br.) Sing.; *H. citrinus* Sing.; *H. corneri* Sing.; *H. campinaranae* Sing.; *H. terraefirmae* Sing.; *H. fuscoalbus* Sing.; *H. depauperatus* Sing.; *H. phyllogenus* Sing. with var. *bahiensis* Sing.; *H. californicus* Sing. ined. apparently also *Clitocybe hydrophora* Pegler and various species described under *Trogia* by Corner.

Subsection *Paraensis* Sing. (1982). Metuloids and/or pseudocystidia present.

Type species: *H. paraensis* Sing.

*H. fuliginosus* (Dennis) Sing.; *H. bisporus* Sing.; *H. mutabilis* Sing.; *H. mesites* Sing.; *H. mycenoides* (Dennis) Sing.; *H. occidentalis* Sing.; *H. subtropicalis* (Sing.) Sing.; *H. immutabilis* Sing.; *H. montanus* Sing.; *H. funebris* (Speg.) Sing.; *H. sphaerosporus* (Dennis) Dennis; *H. eitenianus* Sing.; *H. guaporensis* Sing.; *H. brunneoumbonatus* (Dennis) Sing.; *H. paraensis* Sing.; *H. boliviensis* Sing.; *H. xanthosarcus* Sing.

Sect. 3. *FLOCCIPEDES* (Kühner) ex Sing. (1961). Epicutis without or with only sparse inconspicuous dermatocystidia, formed by repent, smooth, filamentous hyphae often filled with vacuolar pigment. Spores amyloid or inamyloid.

Type species: *H. floccipes* (Fr.) Sing.

Subsection *Spurii* (Kühner) ex Sing. (1961). Spores amyloid; pseudocystidia none.

Type species: *H. scabripes* (Murr.) Sing.

*H. scabripes* (Murr.) Sing.; *H. taxodii* (Murr.) Sing.; apparently also *H. conicus* Bas & Weholt.

Subsection *Lipocystides* Sing. (1982). Spores amyloid; pseudocystidia present.

Type species: *H. lipocystis* Sing.

*H. lipocystis* Sing.; *H. fuscomycelinus* Sing.

Subsection *Floccipedes* (Kühn.) ex Sing. (1961). Spores inamyloid.

Type species: *H. floccipes* (Fr.) Sing.

*H. hygrophilus* Sing.; *H. decipiens* Sing.; *H. heterocystis* Sing.; *H. recedens* Sing.;  
*H. gracilis* Sing.; *H. floccipes* (Fr.) Sing.; *H. gomezii* Sing.

## 100. FILOBOLETUS Henn.

Warburg's *Monsunia* 1: 146. 1900, sensu Hoehnel, em.

Type species: *Filoboletus mycenoides* Henn. sensu Hoehnel.

Syn.: *Laschia*, sect. *Porolaschia* Pat. *Journ. Bot.* 1: 231. 1887. p.p.

*Leucoporus*, sect. *Gelatinosi* Pat. *Essai tax.*, p. 82. 1900.

*Leucoporus*, sect. *Filipedes* Pat., l.c.

*Bactroboletus*, Clements, *Gen. Fungi*, p. 108. 1909.

*Mycenoporella* Van Ov. in Van Ov. & Weese, *Icon. Fung. Malay.* 14-15: 2. 1926.\*

**Characters:** Habit marasmoid-omphaloid, or marasmoid-mycenoid, but suggesting a *Polyporus* because of the configuration of the hymenophore (Pl. 46,2); pileus convex; epicutis consisting of thin repent filamentous hyphae which are either smooth or very finely roughened; hypodermium little differentiated but of considerable diameter, denser than the trama of the pileus; hymenophore distinctly poroid, the pores usually not even arranged in a radial manner so as to suggest the derivation from lamellae, forming a rather deep or a very shallow layer; spore print white; spores hyaline, smooth, ellipsoid to short-ellipsoid, sometimes ellipsoid-oblong or subglobose, amyloid or (in one species) inamyloid\*, wall homogeneous; basidia normal; cheilocystidia not always clearly differentiated from the pseudoparaphyses (which may take the shape of "epibasidium"-bearing basidioles, and remain sterile); rarely similar cystidioid bodies or clavate, often appendiculate elements taking the shape of dermatocystidia near the margin and/or on the disc of some specimens; stipe central, or slightly eccentric, more or less "grafted" to the substratum or truly insititious, without a trace of a pseudorrhiza, subglabrous to pruinose or floccose, not tomentose except sometimes at the base, with numerous dermatocystidia; context consisting of thick-walled hyphae (at least many of them thick-walled), very frequently somewhat gelatinized, at least in some portions of the carpophore (not in the stipe), inamyloid, with clamp connections. On dead wood, more rarely on other dead plant débris (foliage, etc.).

\*The type of *Mycenoporella*, *M. lutea* Van Overeem has not been restudied by me. Topotypic material collected by Lütjeharms (no. 2824) has been studied by Horak (1968), and his analysis corroborates my assumption that it is congeneric with *Filoboletus*, except that the spores (from an alcohol preparation) are said to be inamyloid. The inamyloidity of the spores has later been corroborated.

*Development of the carpophores:* *F. manipularis* is gymnocarpous according to Corner (*Trans. Brit. Myc. Soc.* 37: 270. 1954); see also Heim, *Rev. Myc.* 10: 40, Fig. 24. 1945 (publ. 1946).

*Area:* Tropics, north to Japan and Florida; south to South Queensland.

*Limits:* This genus is sharply separated from other genera of the Mycenaeae by the truly poroid-tubulose hymenophore in most forms, and even where the pores are radially seriate, the cross-walls are of the same breadth as the radial ridges and not merely intervenose. The genus would still be different from the other genera such as *Baeospora* and *Hydropus* even if the hymenophore were more lamellate. Therefore it may be confused with *Polyporus* rather than with other agarics, and it has indeed been confused by Lloyd, but *Polyporus* has cylindric, inamyloid spores.

There may be some question whether or not Höhnel's *Filoboletus mycenoides* is actually, as Höhnel assumed, the genuine species collected for Hennings and described by him. Hennings's type has been destroyed. There is a slight divergence in size when both descriptions are compared but not enough - in a group with great variability in size, and when dealing with Hennings's inaccurate descriptions - to warrant a distinction, certainly not enough to call it "a quite different species" (Donk 1962) without further elaboration. The only material that can still be checked is that collected by Höhnel. Consequently, the only reasonable solution is to admit *Filoboletus* in the sense of Höhnel. Otherwise a clear delimitation of the genus will never be possible even if some material should be found in Java to fit Hennings' diagnosis. Boedijn who knew the basidiomycete flora of Java well, has kindly advised me in this matter; he believed that *Filoboletus mycenoides* Henn. is indeed conspecific with Höhnel's material. This material (FH) is therefore considered as topotype and neotype of *Filoboletus mycenoides* Henn.

As for *F. lutea*, the inamyloid spores are exceptional as is the color of the carpophores. Unfortunately no data have been published on the Melzer reaction of the hyphae of pileus and stipe. Even if the inamyloid spores may suggest *Mycena* sect. *Purae*, the very small true pores (not strongly interwoven lamellae) are like those of *F. gracilis*. Although it seems almost certain that the type of *Mycenoporella* is a *Filoboletus*, a separate section ("Mycenoporella") is not introduced at this time while data on the (pseudo)amyloidity of the tramal hyphae is wanting.

*State of knowledge:* Excepting for the type of *Mycenoporella*, and the embryological and cytological details, all six species are well known.

*Practical importance:* Not known.

## SPECIES

### 1. Species with inamyloid spores (according to Horak).

*F. luteus* (Van Overeem in Van Overeem & Weese) Sing. (*Mycenoporella*, Van Overeem in Van Overeem & Weese).

## 2. Species with amyloid spores.

*F. mycenoides* Henn. sensu Höhnel; *F. manipularis* (Berk.) Sing.; *F. gracilis* (Klotzsch apud Berk.) Sing.; *F. clypeatus* (Pat.) Sing. (*Polyporus obolus* Ell. & Ev.; *F. propullulans* Libonets-Barnes); *F. staudtii* (Henn.) Sing.

### 101. DENNISIOMYCES Sing.

*Anais Soc. Biol. Pernambuco* 13: 225. 1955.

*Type species:* *D. glabrescentipes* Sing.

*Syn.:* *Pleurella* Horak, *N.Z. Journ. Bot.* 9. 1477. 1971.

*Characters:* Habit collybioid-tricholomatoid, sometimes somewhat pleurotoid; dermatocystidia on pileus scattered to numerous but not forming a continuous layer; lamellae with cheilocystidia and pleurocystidia; spores ellipsoid, smooth, thin-walled, amyloid, a cyanophilic; hymenophoral trama regular; stipe stuffed; hyphae of carpophore with clamp connections, inamyloid, pigment-incrusted. On earth and woody humus under trees.

*Development of the carpophores:* Unknown.

*Area:* Neotropical, from Trinidad to Brazil; one species each in California and Europe; probably one in New Zealand.

*Limits:* The dermatocystidia, being occasionally little differentiated and mere hyphal ends, are a mere additional character; but the pleurocystidia are diagnostic on the generic level and serve to distinguish this genus from temperate *Porpoloma* and from *Dermoloma*. Another genus with amyloid spores and pleurocystidia is *Melanoleuca* but this is not even strongly related to *Dennisiomyces* having another type of cystidia, almost amylaceous exosporial amyloidity in the spores, the latter generally showing a plage, and finally, species of *Dennisiomyces* have clamp connections while *Melanoleuca* does not. As for *Hydropus*, obviously the most closely related genus, see there.

*State of knowledge:* Six species, completely known, have been studied by the author.

*Practical importance:* Unknown.

### SPECIES

*D. glabrescentipes* Sing.; *D. griseus* (Dennis) Sing. (*Tricholoma*, Dennis); *D. fulvidiscus* (Murr.) Sing. (c.n. = *Gymnopus fulvidiscus* Murr., *N. Am. Fl.* 9: 368. 1916); *D. fuscoalbus* Sing. ined.; *D. rionegrensis* Sing. ined.; *D. trichodermus* (Joss. apud Kühn.) Sing. (c.n. = *Mycena trichoderma* Joss. apud Kühn., *Encyclop. Mycol.* 10: 689. 1938; *Hydropus*, Sing.); apparently also *Pleurella ardesiaca* (Stevensen) Horak.

## 102. DERMOLOMA (Lange) Sing. ex Herink

*Acta Mus. Boh. Sept. Liberec.* 1: 62. 1959. Sing. *Agar. mycotax.* p. 250. 1951 (no Latin, nom. prov.).

*Type species:* *Tricholoma cuneifolium* (Fr.) Gill.\*

*Syn.:* *Tricholoma* subgen. (?). *Dermoloma* Lange, *Dansk. Bot. Ark.* 8: 12. 1933 (status as subgenus or otherwise not indicated).

*Characters:* Habit collybioid-tricholomatoid. Pileus with an epicutis consisting of a palisadic or hymeniform continuous layer if subisodiametric or at least broad erect elements; cystidia none; hyphae inamyloid, with clamp connections pigment encrusting; spores smooth, amyloid or inamyloid, usually short ellipsoid, broadly ovoid, or short-cylindric, acyanophilic; veil none. On earth, independent of forest trees.

*Development of the carpophores:* Unknown.

*Area:* Europe, South America, Eastern North America, probably also in other (but apparently isolated) regions. One has the impression of a rather ancient group with a contracting general area.

*Limits:* The description given above circumscribes quite clearly the limits of the genus. However, a newly described species, *Tricholoma hygrophorus* Josserand (invalid name) with a looser and less hymeniform epicutis (more like the cellular covering layers known in *Hygrotrama* or *Hydropsus*), relatively longer basidia (al-

\*My suggestion of a type species for Lange's *Dermoloma* has caused M. Josserand to publish on the history of the "case" and its seeming contradictions. The "juridical" phase of the question is very simple: Lange considered his *T. cuneifolium* as part of a "stirpe" and it follows that in elevating the subgenus with its only species to the rank of genus, this only species indicated by Lange, viz. *D. cuneifolium* sensu Lange, is also the type of the genus once this is validly published. This suggestion was made by me with the specification "sensu Josserand i.e. Lange". In view of the fact that Lange does not say whether the spores are amyloid or not, while Josserand and my generic description say they are, my equation *D. cuneifolium* Josserand i.e. Lange is although wrong nomenclaturally, not quite so puzzling as Josserand makes it out to be inasmuch as my elevation in rank was not yet validly published.

It is then a question about the synonymy of Lange's fungus, rather than a simple question of nomenclature which caused Josserand to disagree with this writer. While neither Josserand nor Singer have had authentic specimens of the collection painted and described by Lange, it was quite useless to insist on either Josserand's (= *Tricholoma atrocinereum* sensu Josserand) or Singer's (= *Dermoloma cuneifolium* sensu Josserand) interpretation of 1951. Nevertheless, it appears necessary to draw attention to the fact that Josserand in 1943 describes *T? atrocinereum* as having a "joli gris souris mat et très fondu" color of the pileus (his plate shows an even purer gray) and although he describes the lamellae as colored, paints them rather whitish and besides refers himself to Fries who describes them as white in *T. cuneifolium*. Consequently, I chose to disagree with Josserand as far as his interpretation of Lange's species goes. It is true that the microscopical characters were more in favor of Josserand's opinion, yet there is no security that microscopical details and macroscopical description came from the same specimen, that the epicutis was not studied in scalp by Lange, and that the spores were not indicated somewhat too small as is often the case in Lange's spore measurements (inasmuch as Josserand permits an analogous discrepancy in *Tricholoma sudum*). This is not to say that I may not have been wrong; indeed, a revision of the genus recently carried out by myself on the basis of fresh Dutch material and Fries' original plates show that there are more species than were anticipated and that Lange's *T. cuneifolium* is neither *T. atrocinereum* sensu Joss. nor *D. cuneifolium* sensu Joss. but a third species, *D. cuneifolium* sensu Fries. This, then, is the type of the genus.

though perhaps below the limit characteristic for the hygrophoraceous species, and apparently without intraparietal pigment) brings up the question whether this is not a form transitional between *Neohygrophorus* and *Hygrotrama*, projected into the Tricholomataceae, or rather a *Hydropus*. I am inclined to believe that it is rather the latter, judging by the exact measurements of the spores and basidia given by Josserand (1958), the apparently non-intraparietal and non-incrusting pigment, and the emarginate-adnate lamellae. The "violently" amyloid spores, described as smooth but with some internal granulations make one also think of *Fayodia*. Without having studied this interesting species myself, I cannot make a final judgement.

Kühner (1980) still defends his opinion that *Dermoloma* is congeneric with *Tricholoma*. This is not only a matter of a wider genus concept as generally adopted by Kühner now, but also a question of seeing the affinities of *Dermoloma* in the Tricholomataceae or the Myceneae (or Fayodieae Kühner). It could not enter the Fayodieae of Kühner's because these are defined so that only omphalioid and collybioid species with "mostly" intracellular pigments enter it. On the other hand, the species with collybioid to ± tricholomatoid habit and amyloid spores would enter Kühner's greatly emended concept of *Tricholoma* (which in turn seems to include also species with mycenoid to collybioid habit such as *Callistosporium*).

The close relationship between *Hydropus*, *Dennisiomyces*, and *Dermoloma* and the structure of the epicutis in these three genera show that one can arrive at such a taxonomic result only if extra-European species are totally disregarded. The fact that in *Clitocybe* there is a small group of species with sub hymeniform epicutis (derived from the very special structure of subgenus *Cystoclitus*) is hardly an argument to postulate the same possibility for *Tricholoma*. My insertion of *D. trichodermus* in the type section of *Hydropus* was certainly, as Kühner states, an error, but one should not forget that this error was initiated by Kühner, in his excellent and still irreplaceable *Mycena*-monograph where both the type section of *Hydropus* and *M. trichoderma* are united into one group: *Spuriæ*. Neither is the presence and absence of a hymeniform epicutis in a totally different group - Lyophylleae: *Calocybe* - sufficient reason to postulate the same in a not at all related tribus of Tricholomataceae. Nor is the "pseudoparenchymatic" structure of the hypodermium in any way comparable to the hymeniform epicutis of *Dermoloma*. If Kühner had taken the trouble of expressing his 1980 classification in form of a key with due attention to "exotic" species and genera, he might have found that his extremely valuable contributions to modern taxonomy are not producing a more "natural" classification than the one presented in the present work.

*State of knowledge:* Eight species are now recognized in *Dermoloma*.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *DERMOLOMA*. Spores inamyloid.

*Type species:* *D. cuneifolium* (Fr.) Sing. ex Herink.

*D. atrocinereum* (Pers. ex Pers.) Herink; *D. cuneifolium* (Fr.) Sing. ex Herink; *D. yungense* Sing.; *D. coryleti* Sing. & Cléménçon, apparently also *D. inconspicuum* Dennis, *D. emiliidlouhyi* Svrček.

Sect. 2. *ATROBRUNNEA*. Spores amyloid.

Type species: *D. atrobrunneum* (Dennis) Sing. ex Herink.

*D. atrobrunneum* (Dennis) Sing. ex Herink; *D. josserandii* Dennis & Orton; *D. aposcennum* Sing. ined.; *D. spec.* (*D. josserandii* Sing. sensu Sing. 1969); apparently also *D. pragense* Kubička ined. and *D. griseocarneum* Pegler.

Note: Several species inserted here in the past, but apparently lacking intraparietal and incrusting pigment are of doubtful position and in need to reexamination: *D. hygrophorus* Joss. (see under "Limits" above) and *D. hemisphaericum* (Stevenson) Horak.

### 103. XEROMPHALINA Kühn. & Maire

apud Konr. & Maubl., *Icon. Sel. Fung.* 6: 236. March 1934 as *Xeromphalia\**; *Bull. Soc. Myc. Fr.* 50: 18. Aug. 1934, as *Xeromphalia*.

Type species: *Xeromphalina campanella* (Batsch ex Fr.) Kühn. & Maire.

Syn.: *Omphalopsis* Earle, *Bull. N. Y. Bot. Gard.* 5: 426. 1909, non Grev.

*Valentinia* Velen., *Nov. mycol.*, p. 38. 1939\*\*.

*Heimiomyces* Sing.; *Lloydia* 5: 128. 1942.

?*Phlebomarasmius* Heim, *Rev. Myc.* 32: 203. 1967.

Characters: Habit of the carpophores omphalioid or omphalioid-marasmoid also collybioid; pigment intercellular, incrusting the walls, bright colored; pileus with initially somewhat incurved margin; epicutis consisting of radially arranged, repent, non-diverticulate hyphae, with or without dermatocystidia or palisade; color of the pileus fulvous, vinaceous, etc.; hypodermium, trama (including the hymenophoral trama) with pigment-incrustations which often turn pink to red with alkali; hymenophore lamellate (but sometimes sinuate, intervenose); lamellae broadly adnate to deeply decurrent, colored; hymenophoral trama regular, its hyphae close, rather voluminous, subparallel and axillarily arranged, with slightly thickened walls; basidia normal; cystidia present on the edge and frequently on the sides of the lamellae, yet in some individuals not very frequent or not very conspicuous, in others very numerous and never conspicuous, in still others rather conspicuous, hyaline, rarely pale stramineous, generally thin-walled; spores hyaline, amyloid, smooth, acyanophilic, with homogeneous wall, ellipsoid, oblong, or cylindrical; spore print white when fresh; above the repent epicuticular hyphae frequently with more or less conspicuous dermatocystidia; trama of the pileus monomitic, hyphae inamyloid, with

\*The spelling *Xeromphalia* has here been taken as a printing error; it does not show up anywhere else in the work or in the index.

\*\*With *Cantharellus valentini* as type. *V. vacini* is *Gerronema albidum* (Fr.) Sing.

clamp connections; stipe either eccentric or more often more or less central, never white, never glutinous, with fulvous colored basal tomentum which is always present, often very conspicuous and strigose (ascending along the surface of the stipe, becoming shorter toward the middle of the stipe and reduced from there upward to a yellowish pruina), never insititious nor arising from a basal disc or a pseudorrhiza; veil none; consistency, especially of the stipe, very frequently toughish, even reviving; on needles, sticks, dead and living wood, buried wood and roots, and on humus. See Pl. 80,2.

*Development of the carpophores:* Gymnocarpous in *X. campanella* according to Hintikka (1957); cultural characters have been studied by O.K. Miller (in Petersen (1971)).

*Area:* Temperate zones of both hemispheres and tropical-montane zone.

*Limits:* As now defined by the key characters and the generic description the genus is well delimited; it differs from the similar genus *Flammulina* by microchemical, developmental and anatomical characters. Later additions - with the exception of the genus *Heimiomyces* - had to be eliminated (such as *Omphalia typhae* Schweers, *Omphalia kalchbrenneri*, *X. mesospora*, and *X. picta*) and are better placed in *Mycena*, *Pseudoomphalina* or *Baeospora*.

*State of knowledge:* Nine species are now admitted in *Xeromphalina*. Several additional species were described by Horak from Indomalaya and Australasia (*Sydowia* 32: 131-153. 1979) and India (*Sydowia* 33: 104. 1980). These were not studied by me.

*Practical importance:* *X. campanella* seems to be so exclusive on conifer wood that it may be used by foresters and ecologists as a reliable indicator of coniferous wood even in badly decayed condition.

## SPECIES

Subgenus 1. **Xeromphalina.** (Subtrib. and sect. - 1821 resp. 1838 - *Mycenarii* Fr.; sect. *Eu-Xeromphalina* A.H. Smith 1923). Habit omphaloid; hypodermium with not distinctly glassy-appearing elements; dermatocystidia on pileus present or absent.

*Type species:* *X. campanella* (Batsch ex Fr.) Kühner & Maire.

*X. caulinialis* (With. ex Fr.) Kühner & Maire; *X. campanella* (Batsch ex Fr.) Kühner & Maire; *X. kauffmanii* A.H. Smith; *X. austroandina* Sing.; *X. orickiana* (A.H. Smith) Sing.; *X. helbergeri* Sing. in Sing. & Digilio (*X. curtipes* Hongo); *X. fellea* Mre & Malençon (*X. amara* Horak & Peter); obviously also *X. yungensis* Sing. (ined.), *X. racemosa* Stevenson, *X. fraxinophila* A.H. Smith.

Subgenus 2. **Heimiomyces** (Sing.) Sing. (1942 as genus) (sect. *Heimiomyces* A.H. Smith). Habit collybioid; hypodermium glassy; dermatocystidia of pileus numerous, forming an almost continuous turf in youth, or else many dermatocystidia branched.

*Type species: Agaricus rheicolor* Berk. (= *Xeromphalina tenuipes*).

Sect. *FULVIPES* O.K. Miller (1968). Spores narrow and often allantoid; dermatocystidia "antler-like", branched.

*Type and only known species: X. fulvipes* (Murr.) A.H. Smith.

*Note:* An apparently closely related species (*X. longispora* Sing. ined.) occurs in the Zaire Republic (ex-Belgian Congo). Pl. 80,2.

Sect. *HEIMIOMYCES* A.H. Smith. Spores ellipsoid, larger and broader than in sect. *Fulvipes*; dermatocystidia dense, often fasciculate, mostly simple.

*X. tenuipes* (Schwein.) A.H. Smith (Collybia, Sacc.; Collybia rheicolor (Berk.) Sacc.; Heliomyces, Speg.; Micromphale, Dennis; Heimiomyces, Sing.; Collybia melinosarca (Kalchbr.) Sacc.; C. cayennensis (Mont.) Sacc.; Marasmius amabilipes Peck; Collybia aurantiella (Speg.) Sacc.; Galera hilariana (Mont.) Sacc.; Crinipellis velutipes Stevenson; Collybia neovelutipes Hongo); apparently also *Phlebomarasmius pilosus* Heim.

#### 104. **BAEOSPORA** Sing.

*Rev. Myc.* 3: 193. 1938.

*Type species: B. myosura* (Fr. sensu Quél., Ricken) Sing.

*Characters:* Habit of the carpophores collybioid, rarely subpleurotoid; pileus with initially incurved margin, hygrophanous or subhygrophanous; pigment, if present, either intracellular or intercellular and incrusting, brown to melleous, or (macroscopically) violet; epicutis and hypodermium well differentiated or little differentiated, the epicutis consisting of more or less radially arranged, filamentous, repent hyphae, but some of the hyphal ends rather ascendant or erect, and then generally transformed into dermatocystidioid excrescencies which, however, are often scattered on the surface of the pileus, but, especially on the margin, may form a hymeniform layer; hypodermium consisting of somewhat larger hyphae; hymenophore lamellate, lamellae narrow, subdecurrent, adnate, or adnexed to subfree, crowded, pallid or somewhat lilac; hymenophoral trama irregular-subintermixed to regular, consisting of elongated hyphae; basidia small, normal; cystidia present but often very scattered, many assuming the characteristics of oleocystidia, and then these appearing on the heteromorphous edges assuming the character of cheilocystidia; spores (Pl. 48,1) hyaline, smooth, very small (to 6 µm), subglobose to cylindric, amyloid, with thin, simple acyanophilic wall; subhymenium forming a thin layer, intermixed-subcellular, consisting of extremely small elements; stipe central or eccentric, with a pseudorrhiza or without it, subequal above the substratum, with dermatocystidia (hairs); basal tomentum mostly white, never fulvous; context pallid to lilac, consisting of inamyloid hyphae with clamp connections. On wood, on cones of conifers, also on other similar substrata buried in the earth.

*Development of the carpophores:* Unknown.

*Area:* Northern temperate zone, more species in the tropics.

*Limits:* The genus has initially been conceived somewhat too widely including species with amyloid tissue, such as *Pseudobaeospora oligophylla*. By excluding these species (Singer 1942), we obtain a very homogeneous, natural small group of species to be retained in *Baeospora*. This genus is then parallel to *Xeromphalina*, obviously the phase of a phylogenetical development where the hymenophore has become non-decurrent, and the spores smaller. There is no difficulty in delimiting the genus *Baeospora* in its present outline. *Hydropus* differs in having cystidia and dermatocystidia of another type, mostly broader subhypodermial hyphal cells and no encrusting yellow matter. *Collybia* (sect. *Vestipedes*) differs, contrary to what is stated by Kühner (1980) not only by the inamyloid spores but by several other characters which include the type (or absence) of dermatocystidia, usually found in *Baeospora*, the different type (or absence) of cystidia - characters that probably induced Kühner earlier to treat the genus in *Mycena*. The existence of a pleurotoid species in *Baeospora* is a further indication that *Baeospora* is not related to *Collybia* where pleurotoid habit is unknown.

*State of knowledge:* The six species entering *Baeospora* are completely known except for the development of the carpophores.

*Practical importance:* None.

## SPECIES

*B. myosura* (Fr. sensu Quél.) Sing. (*Collybia*, Quél.; *Mycena*, Kühner; *Collybia strobilina* Velen.; *Collybia friesii* Bres.) and its variety var. *favrei* Sing. [*Baeospora myosura* ssp. *varicosa* (Fr. sensu Boudier, non Fries) Favre]; *B. myriadophylla* (Peck) Sing. (*Collybia*, Peck; *Mycena*, Kühner; *Collybia lilacea* Quél.; *Collybia teleojanthina* Métrod); *B. pleurotoides* (Dennis) Sing. (*Collybia*, Dennis); *B. brunneipes* (Sing. in Sing. & Digilio) Sing. (*Heimiomyces*, Sing. in Sing. & Digilio); *B. pruinatipes* (Sing. in Sing. & Digilio) Sing. (*Heimiomyces*, Sing. in Sing. & Digilio); *B. pallida* Sing.

## 105. RESINOMYCENA Redhead & Singer

*Mycotaxon* 13: 151. 1981.

*Type species:* *Agaricus rhododendri* Peck.

*Characters:* Habit omphaloid to mycenoid, with adnate to decurrent lamellae; stipe cartilaginous, not insititious; hyphae (where not subgelatinous) weakly to distinctly pseudoamyloid, or with inamyloid ones intermixed, with thin wall, with clamp connections, not forming a typical *Mycena*-structure; epicutis of pileus and stipe with scattered or clumped oleocystidia, often intermixed with filamentous or rameous hyphal elements, these suberect, tangled or decumbent, not diverticulate or with *Marasmiellus*-structure; spores larger than 5.3  $\mu\text{m}$  and reaching up to 12.5  $\mu\text{m}$ , thin-

walled, amyloid, smooth, with entire wall, hyaline, acyanophilic; ellipsoid, ovoid, or fusoid; basidia normal; cystidia absent or not numerous and like the cheilocystidia, the latter like the oleocystidia eventually with a resinous granular covering, at least a scanty one; pigments none or inconspicuous or else incrusting the hyphae, the exudations of the oleocystidia often ± yellowish. On leaf and needle litter, on small fragments of cones, on dead leaves and branchlets, often among mosses; in temperate zones, reaching the alpine zone.

*Development of the carpophores:* Unknown.

*Area:* Northern hemisphere, mainly in North America, rare in Europe.

*Limits:* The species may be mistaken for *Mycena*, *Hydropus*, and *Baeospora*, and seem to be very closely related to each other. They can be generically determined by the characters indicated in the key. Their generic delimitation has been discussed by Redhead & Singer l.c.

*Practical importance:* Unknown.

## SPECIES

*R. rhododendri* (Peck) Redhead & Sing.; *R. saccharifera* (Berk. & Br.) Redhead (*R. kalalochiensis* (A.H. Smith) Redhead & Sing.; *Delicatula quisquiliaris* (Joss. ex Bon); *R. montana* Redhead & Sing.; *R. acadiensis* Redhead & Sing.; *R. brunnescens* Redhead & Sing.; *R. pyrenaica* Sing. (n.n. = *Marasmius rhododendri* Sing., *Collectanea Botan.* 1: 224. 1947).

### 106. FAYODIA Kühner

*Bull. Soc. Linn. Lyon* 9: 68. 1930; em. Sing. *Rev. Myc.* 1: 279. 1936.

*Type species:* *Omphalia striaeapilea* sensu Ricken (= *Fayodia gracilipes* (Britz.) Bresinsky & Stangl.).

*Syn.:* *Myxomphalia* Hora, *Trans. Brit. Mycol. Soc.* 43: 453. 1960.

*Stachyomphalina* Bigelow, *Mycotaxon* 9: 41. 1979.

*Gamundia* Raithelhuber, *Metrodiana* 8: 34. 1979.

*Heterosporula* (Sing.) Kühner, *Bull. Soc. Linn. Lyon* 49: 172. 1980.

*Characters:* Habit of the carpophores omphaloid (or more rarely nearly collybioid to mycenoid); pigment dark, dusky and dull (gray, umber, sepia-fuscous to nearly blackish, or more rarely absent, if present - mostly intracellular, but in some species also intraparietal or even incrusting; epicutis of the pileus consisting of smooth and repent hyphae, forming a cutis or an ixocutis, rarely some hyphal ends somewhat ascendant; hypodermium of voluminous cells often present, epicuticular elements hyphous, usually smooth, but occasionally with diverticula of the *Mycena*-type; trama monomitic, inamyloid, rarely vaguely pseudoamyloid, with clamp connections, rarely without clamps; lamellae ascendant to descendant, also often frankly decurrent; basidia normal but sometimes bisporous; pseudocystidia or cystidia

sometimes present, but sometimes only cheilocystidia present (and even these at times not very conspicuous); spores hyaline, oblong, ellipsoid or globose, with somewhat thickened heterogenous or at any rate non-smooth wall which is either amyloid or inamyloid, partly cyanophilic insofar as the thick-walled spores have some cyanophilic layer and the imbedded (?) ornamentations are somewhat to distinctly cyanophilic and the upper surface usually more or less punctulate (much like in *Crepidotus* sect. *Echinospori*), in EM sections (cf. M. Besson, *C.R. Acad. Sci. Paris* 268: 3167-9, pl. 1-2. 1969) showing an ornamented layer different from the subjacent layer (the coriotunica in Clément's terminology); the periphery smooth in most spores and at times amyloid with the subjacent layers inamyloid (in subgenus I); stipe moderately thick or rather thin, usually central, solid or becoming tubulose, not insititious. On decayed trunks, logs, fallen branches, charcoal, on soil, and on leafmold.

*Development of the carpophores:* Gymnocarpous and stipitocarpous in *F. maura* (Watling).

*Area:* Almost cosmopolitan.

*Limits:* Repeated emendations of the genus have produced a genus much larger than originally conceived, but undoubtedly homogeneous and easily delimited. The fine structure of the spore wall is the ultimate diagnostic concept which infallibly separates this genus from all other genera of the Mycenaceae. In the white-spored agarics, there are only few instances of similarly heterogenous spore walls: *Hygrocybe transformabilis* Sing. among the species with inamyloid spores, and *Porpoloma metapodium* (Fr.) Sing. among the species with amyloid spores. The first of these species differs from *Fayodia* subgenus *Heterosporula* in the bright pigment of the fresh carpophores, the glutinous pileus and stipe, the larger or not thickwalled basidia. *Porpoloma metapodium* is thick-fleshy and tricholomatoid, reddening, and non-hygrophanous; its epicutis is trichodermial and quite different from that of the *Fayodias*, especially those of subgenus *Myxomphalia*.

Our conclusion that the amyloid-spored subgenus *Myxomphalia* and the inamyloid-spored subgenus *Heterosporula* are congeneric is confirmed by the fact that the one species studied in each subgenus (*F. maura* and *F. striatula*) belongs to the same minority type of sexual development among Tricholomataceae: Bipolar heterothallism (Kühner 1979).

Some authors give more weight than we do to the exact structure of the spore walls and their amyloidity. They therefore consider the first subgenus as *Fayodia* sensu stricto, the second as (genus) *Myxomphalia*, the third as *Stachyomphalina* and the last remains neglected. What appears like ornamentation type XI in subgenus III is in EM (as by the way in *Crepidotus*) an ornamentation of free spinules but a fugacious perisprium may be discovered in further studies. As for *Myxomphalia*, the spore wall is ornamented as has been confirmed by Kühner (1980). There is no reason, at present, to overemphasize the spore differences or to dismember the genus *Fayodia* as here delimited.

A species which I have determined as *Mycenella eriopus* (Sacc. & Syd.) Sing (which may not actually be identical with the type of that species) differs from *Mycenella* in

a spore ornamentation more like that of *Heterosporula*, but with the spinules projecting beyond the external spore wall and the cystidia strongly metuloid. The position of that species is not fully clear at present, but it may perhaps be better classified in *Fayodia* than in *Mycenella*. According to the spores, *F. albidula* (Pat.) Pegler has already in 1962 been placed in sg. *Heterosporula*. It has no pleurocystidia. Both *M. eriopus* sensu Sing. and *F. albidula* may be considered the type of sections within *Heterosporula*.

**State of knowledge:** While 11 species of *Fayodia* are now well known it would still be desirable to reread all Myceneae with non-smooth and non-homogenous spore wall monographically, with special consideration of the wall structure under EM and SEM. Until this is done, the present structure of the genus seems quite satisfactory.

**Practical importance:** *F. maura* contains an antibiotic substance.

## SPECIES

**Subgenus I. *Fayodia*.** Cheilocystidia distinct; pleurocystidia present or absent; phaeocystidia none; lamellae mostly not distinctly arcuate-decurrent, spores usually  $> 6.5 \mu\text{m}$  (at least many), with the exosporium amyloid, acyanophilic, middle layer strongly and distinctly heterogenous; surface layers of pileus and stipe not gelatinizing; clamp connections present. Pl. 50,4; 80,1 (spores).

**Type species:** *F. bisphaerigera* (Lange) Kühner.

*F. gracilipes* (Britz.) Bresinsky & Stangl (*F. bisphaerigera* (Lange) Kühner); *F. tetrasphaerigera* Sing.; *F. tenuisperma* Sing.; obviously also *F. anthracobia* (Favre) Kühner & Romagnesi.

**Subgenus II. *Myxomphalia*** (Kühner) Sing. (1943) ex Sing. 1961. Cheilocystidia distinct; pleurocystidia present or absent; phaeocystidia none; spores  $< 6.8 \mu\text{m}$ , with the walls generally strongly amyloid, slightly but distinctly ornamented, firm and smooth to slightly uneven; lamellae adnate to decurrent; external hyphae of the pileus forming an ixocutis and pileus strongly viscid to glutinous, more rarely cutis not gelatinized and pileus dry.

**Type species:** *F. maura* (Fr.) Sing.

*F. maura* (Fr.) Sing.; *F. invita* (Karst.) Sing.; *F. marthae* Sing. & Clémenton; *F. agloea* Sing. & Passauer; obviously also *F. alutacea* Bigelow.

**Subgenus III. *Heterosporula*** Sing. (1961). Differing from subgenera I and II in entirely inamyloid spore wall; phaeocystidia none; clamp connections present.

**Type species:** *F. pseudocclusilis* (Joss. & Konr.) Sing.

*F. striatula* (Kühner) Sing. (Rhodocybe, Kühner; Omphalia, Kühner & Romagnesi; Clitocybe, Orton; Mycena cineraria A.H. Smith); *F. pseudocclusilis* (Joss. & Konrad) Sing.; *F. xerophila* Lüthi & Röllin; *F. albidula* (Pat.) Pegler; probably also *Mycenella eriopus* (Sacc. & Syd.) Sing. sensu Sing.

Subgenus IV. **Clemenconia** Sing. (1972). Differing from subgenus III in the presence of phaeocystidia and the absence of clamp connections.

Type and only known species: *F. deusta* Sing. & Cléménçon.

Reduced series: 107. **CELLYPHA** Donk

*Persoonia* 1(1): 84. 1959.

Type species: *Cyphella goldbachii* Weinm. (sensu Donk).

Syn.: *Cyphella* subgen. *Glabrotricha* Pilát, *Ann. Mycol.* 23: 148. 1925.

**Characters:** Habit pezizoid, erect to pendulous, small, typically sessile, sterile surface rather conspicuously tomentose, margin not involute, tomentum consisting of irregularly bent and ramified hyphae, from these emerge numerous hair-like terminal members which are hyaline, thin-filamentous and capitate or claviculate at their tips, forked or more frequently simple, moderately firm-walled (not thick-walled) or quite thin-walled, inamyloid; in between these hairs are hyphae which emit short side-branches, bulges or knots; the sterile surface convex, the rim slightly incurved at first, fimbriate; hymenial surface either quite smooth, or in age becoming once or twice ridged by lamella-like folds, or wrinkled, white or cream color; basidia clavate, or slightly uteriform, without siderophilous granulation, 2-4-spored or 4-spored; cystidia and pseudocystidia none; spores hyaline, narrow,  $> 6 \mu\text{m}$  long, inamyloid; trama monomitic, some hyphae inflated, all inamyloid, with clamp connections, not gelatinized; pigments none, but the elements of the epicutal layer often covered by a resinous, melleous-succineous, incrusting pigment; on dead sticks and leaves, often on Monocotyledones (*Holcus*, *Carex*, *Bambuseae*, *Palmae*) but also on dicotyledonous hosts, even on bark and fallen branches of shrubs and trees.

*Development of the carpophores:* Unknown.

*Area:* Europe, North and South America.

*Limits:* As all monotypic genera, *Cellypha* is difficult to delimit, but appears to be sharply separated from other "cyphellaceous" genera, including *Pleuromycenella*, and from *Hemimycena*.

*State of knowledge:* The only species known is well and completely described and illustrated.

*Practical importance:* Unknown.

SPECIES

*C. goldbachii* (Weinm.) Donk; possibly *Cyphella paraguayensis* Speg. (see *Darwiniana* 14: 17-18. 1966).

*Sydowia*, Beih. 7: 27. 1973.

Type species: *P. circularis* Sing.

Syn.: *Flabellimycena* Redhead, Can. Journ. Bot. 62: 886. 1984.

**Characters:** Small pleurotoid, carpophores with eventually strictly lateral stipe, or laterally attached and sessile, pigment-less or yellow all over; hymenophore absent, or a few low radial veins present; sterile surface convex, with the epicutis less differentiated than in *Cellypha*, but near margin there are some, often capitate, dermatocystidia and some more or less obtusely diverticulate hyphal cells, these thin-walled, non-gelatinized, non-incrusted; immediately below some broad, rather voluminous (to 30 µm diam.) hyphae which are also present all through the monomitic and inamyloid, thin trama which is likewise not gelatinized, and with numerous clamp connections, but there are also some filamentous, non-inflated hyphae present; basidia clavate, 2-4-spored or 4-spored, without siderophilous granulation; cystidia none; pseudocystidia none; spores ellipsoid or broadly ellipsoid, hyaline, with homogeneous inamyloid wall, not reaching 10 µm in length; on living moss and woody litter particles among moss.

**Development of the carpophores:** Unknown.

**Area:** Mexico to Colombia.

**Limits:** The broad tramal cells, and often stipitate\* carpophores differentiate this genus from the genus *Mniopetalum* which is also white and moss-inhabiting. The less developed epicutis, the different spore type, and the lateral, often stipitate attachment differentiate this genus from *Cellypha*. Both the latter and *Pleuromycenula* are apparently closely related to *Hemimycena*. While the present author maintains that the three species here enumerated constitute a well defined separate genus, Redhead (1984) considers the type species to belong in his emended genus *Rimbachia* (cf. discussion there), *P. circularis* in *Helotium* (i.e. *Hemimycena*), and *P. flava* in a separate new genus *Flabellimycena*.

**State of knowledge:** Three species are known.

**Practical importance:** Unknown.

## SPECIES

*P. circularis* Sing.; *P. ellipsoidea* Sing.; *P. flava* Sing.

\*Only *P. ellipsoidea* is sometimes with, sometimes without stipe, not astipitate as stated by Redhead (1984, p. 867); other species always stipitate.

*Mycologia* 73: 504. 1981.

Type species: *M. theobromicola* Sing.

**Characters:** Habit cyphelloid, the pileus reduced to an isolated cup, not rising from a common stroma, white throughout, with glabrous or subglabrous sterile surface but the margin ciliate sub lente, with smooth hymenial surface; stipe none, pseudo-stipe none or very short, white, glabrous or subglabrous; context extremely thin; spores medium sized, ellipsoid to oblong, with conspicuous oblique hilar appendage, hyaline, smooth, inamyloid, acyanophilic; basidioles  $\pm$  fusiform; cystidia none but cystidiform marginal cells along the rim of the cup numerous,  $20-29 \times 4.5-6.5 \mu\text{m}$ , either broadly rounded above or with an apical appendage, the main body subcylindric to more frequently clavate, beset (excepting the appendage) with a dense, fine diverticulation of the type seen in the acanthocysts of *Favolaschia* or the cheilocystidia of some *Mycenas*, entirely hyaline, appendage up to  $45 \mu\text{m}$  long, all thin-walled; hyphae hyaline, not gelatinized in any part, without clamp connections in the type species, all thin-walled, cylindric to filamentous, in part interwoven, in part parallel or subparallel, some hyphal cells distinctly inflated to 15, rarely  $20 \mu\text{m}$ , inamyloid. Epicutis of repent hyphae, at least on the outside beset with diverticula (as the marginal hairs), some dermatocystidia like the marginal hairs also at the base of the carpophores; pigment none. On dead pods of *Theobroma*.

Development of the carpophores: Unknown.

Area: Bahia, Brazil.

Limits: The *Mycena*-like hyphae of the epicutis are unique in the reduced series of *Myceneae*.

State of knowledge: Only one species is known thus far.

Practical importance: The carpophores are only found on dead pods of cacao in the heaps near plantations. Unless there is an imperfect parasitic form of this the fungus described above does not seem to have any importance as a pathogen.

## SPECIES

*M. theobromicola* Sing.

Tribus *Pseudohiatuleae* (Sing.) Sing.

*Agar. mod. tax.* 3rd ed. p. 412. 1975.

Type genus: *Pseudohiatula* Sing.

**Characters:** Basidia not siderophilous and generally not longer than five times the

length of the spores; habit collybioid or mycenoid; hymenophore present, lamellate; epicutis often hymeniform, or initially fragmentarily subhymeniform, often with conspicuous dermatocystidia, or else epicuticular elements fasciculate and agglutinate to form furfuraceous to subpyramidal coverings on pileus (and stipe) and then not rising from a gelatinous layer nor the epicutis itself gelatinized, but where the surface is glabrous, the epicuticular elements may rise from a gelatinized hypodermium, in this case the epicutis often reduced to numerous dermatocystidia not forming a strictly hymeniform layer, and the pileus tending to be viscid or glutinous; epicuticular elements never pseudoamyloid; hymenophoral trama bilateral and remaining so until the button-state is reached or permanently, but not becoming strictly regular even in age or soon becoming regular, often partially gelatinized; trama fleshy to soft-membranous, monomitic, with or without clamp connections; base of the stipe insititious or with a basal mycelium fibrillose; cystidia (and/or pseudocystidia) more frequently present than absent, and often conspicuous on the sides of the lamellae; spores hyaline, white in print, inamyloid or (not persistently) amyloid, smooth with homogeneous thin to firm wall, subglobose or (mostly) ellipsoid, ventricose, fusoid, oblong, or cylindrical, acyanophilic, in firm-walled spores sometimes with a thin outermost cyanophilic layer (in *Callistodermium*); carpophores rarely without any pigment; latex none; lichenization and ectomycorrhiza never observed, most species lignicolous.

#### KEY TO THE GENERA

- A. Pileus glabrous to finely pruinose, viscid or not, yellow, brown, orange, epicutis of isolated dermatocystidia with thin or moderately inconsistently thickened, often pigmented wall or rising from a hymeniform or palisadic layer over gelatinized hypodermium; lamellae subclose or close; spores inamyloid; stipe often vellereous, not insititious; hymenophoral trama weakly bilateral; development paravelangiocarpous; spores mostly binucleate, inamyloid. 110. *Flammulina*, p. 435
- A. Pileus glabrous, velutinous, or floccose, not viscid, spadiceous or fuscous-fuliginous or bright colored (red, yellow, olive etc.), epicutis hymeniform or subhymeniform, but often producing a floccose outer layer or else conspicuous, thick-walled and projecting dermatocystidia; hypodermium non-gelatinized or subgelatinous to gelatinous; lamellae distant or subdistant; spores amyloid or inamyloid; stipe often pubescent from dermatocystidia, or floccose-furfuraceous, insititious or not; hymenophoral trama distinctly and consistently bilateral; development of the carpophores and number of nuclei in spores unknown for many species. 110. *Flammulina*, p. 435
- B. Pileus glabrous, often rugose, thin, spadiceous or fuscous-fuliginous, with hymeniform epicutis and numerous, conspicuous, thick-walled, projecting dermatocystidia; spores amyloid or inamyloid, not longer than 8  $\mu\text{m}$ ; lateral trama of the hymenophore gelatinized; base of stipe insititious or weakly fibrillose from a slight basal mycelium; habit mycenoid or collybioid. 111. *Pseudohiatula* p. 436
- B. Pileus glabrous, or more frequently flocculose or floccose or velutinous, moderately thin, colored as above, or more frequently ochraceous or bright red, orange, yellow, olive, lateritious, deep chestnut etc.; with hymeniform or palisadic or trichodermial or epithelial epicutis and its elements thick- or thin-walled, with or without not or slightly projecting dermatocystidia (unless these form the floccose covering); spores inamyloid, small, medium sized or up to 16  $\mu\text{m}$  large; lateral stratum of the lamellae gelatinized or not excepting the edge-near region in some species; base of stipe insititious or not; habit collybioid.
- C. Spores  $> 5 \times 3.5 \mu\text{m}$ ; epicutis trichodermial, subhymeniform, hymeniform, often dissociating into floccons, not becoming violet or purple in alkaline medium; cystidia present on the sides of the lamellae unless the lateral stratum of the hymenophoral trama is gelatinized

and/or clamp connections are absent; lamellae white to beige or yellowish white to reddish when fresh. Lignicolous.

112. *Cryptotrama*, p. 437

C. Spores  $< 5 \times 3.8 \mu\text{m}$ ; epicutis epithelial to trichodermial and then with thickish walled elements which are brown in acid media and often become purple or violet in KOH and NH<sub>4</sub>OH, or else epicutis a trichodermial palisade; cystidia none; cheilocystidia numerous; hymenophoral trama not gelatinized in any part; lamellae cream yellow, olive or cinnamon brown; on earth or on roots or small woody chips.

113. *Callistodermatium*, p. 440

## 110. FLAMMULINA Karst.

*Symb. Myc. Fenn. 30, Meddel. Soc. Fauna Flora Fenn. 18: 62. 1891.*

*Type species: Collybia velutipes* (Curt. ex Fr.) Kummer.

*Syn.: Collybidium* Earle, *Bull. N. Y. Bot. Gard.* 5: 428. 1909.

*Myxocollybia* Sing., *Beih. Bot. Centralb.*, Abt. B 56: 162. 1936.

*Characters:* Habit collybioid; pigment usually present; pileus viscid or dry glabrous, with dermatocystidia; lamellae usually yellowish, rounded-adnexed or adnate-sinuate, moderately thin; spore print pure white; spores (pl. 48,2) hyaline, with smooth homogeneous wall, binucleate, inamyloid, acyanophilic, up to  $12 \mu\text{m}$  long, ellipsoid to oblong; cystidia on the sides of the lamellae present or absent; hypodermium gelatinized or at least subgelatinous, lateral stratum of the weakly and inconsistently bilateral hymenophoral trama weakly gelatinized or subgelatinous; and often a subhymeniform or hymeniform epicutis immediately above the gelatinized hypodermium, dermatocystidia rising between the epicuticular elements which may be obliterated, and then dermatocystidia solitary; stipe often vellereous, not insititious, pigmented; context of the pileus rather thin to rather thick, fleshy, monomitic, consisting of inamyloid hyphae with clamp connections. Lignicolous, rarely on roots of *Ononis*.

*Development of the carpophores:* Hemiangiocarpous (Moss 1923), interpreted as paravelangiocarpous and pileostipitocarpous by Reijnders (1963) (see Williams & al., Chapter 13).

*Area:* Almost cosmopolitan, certainly in the temperate zones of both hemispheres and in the neo- and paleotropics.

*Limits:* It was rather the isolation of the genus than its close relationships which caused mycologists to be uneasy about the affinities of *Flammulina*. Since the other genera of the tribus Pseudohiatuleae have been studied more in detail, it appears that *Flammulina* is most closely related to *Cryptotrama*. It can be easily recognized by the key characters. It should, however, not be confused with *Xeromphalina* sub-gen. *Heimiomyces* which may be very similar macroscopically but differs by the amyloid spores and many other characters. If, because of the weakly bilateral trama, a *Flammulina* would be mistaken for a representative of the tribus Marasmiaceae, there might be confusion with the genus *Oudemansiella* or *Physocystidium* but a careful comparison with the generic diagnosis of the latter genera will show that there are considerable differences. *Oudemansiella* has very different spores which are broader, weakly cyanophilic, and the structure of the epicutis is not identical nor are the pigments of the glutinous species; the hilum of the spores is of the

open-pore type while in *Flammulina* it is nodulose. *Physocystidium* has a very different epicutis.

**State of knowledge:** Embryologically and cytologically completely known is only *F. velutipes*, the type species. But the other species, both macro- and microscopically studied in detail, are sufficiently similar to consider them congeneric, which brings the number of species up to three.

**Practical importance:** The type species is an excellent edible fungus (if the stipes are discarded), especially valuable since it forms its carpophores in winter when other mushrooms are rare; it is grown commercially and sold as "enoki". It is reported to have antitumor activity (Ikekawa et al. & Komatsu et al.).

## SPECIES

*F. velutipes* (Curt. ex Fr.) Sing.; *F. callistosporioides* (Sing.) Sing.; *F. ferrugineolutea* (Beeli) Sing.; obviously also *F. ononidis* Arnolds; *F. fennae* Bas.

### 111. PSEUDOHIATULA (Sing.) Sing.

*Notulae Crypt. e Sect. Crypt. Ac. Sc. U.S.S.R.* 10-12: 8. 1938.

**Type species:** *P. cyatheaee* (Sing.) Sing.

**Syn.:** *Mycena*, Subg. *Pseudohiatula* Beih. *Bot. Centralbl.*, Abt. B. 56: 165. 1936.

**Characters:** Habit of the carpophores mycenoid or collybioid; pileus non-viscid, convex, without macroscopically visible hairs, but under a lens or under the microscope, hairs or dermatocystidia often very conspicuous, projecting from among elements that form a hymeniform layer, with thick wall, inamyloid (similar dermatocystidia on the stipe forming its pubescence); lamellae usually white (or showing some gray or bister tone), subdistant or distant, narrowly adnexed to subfree; spore print white; spores hyaline, ellipsoid or ventricose, with homogeneous, thin, smooth, acyanophilic wall, small to medium sized (not larger than 8.5  $\mu\text{m}$  long); basidia normal, 2-4-spored or 4-spored; cystidia thin-walled or metuloid (pseudoamyloid or inamyloid), projecting; trama monomitic, but the lateral stratum of the hymenophoral trama gelatinized, hymenophoral trama bilateral (distinctly so); clamp connections present but often scarce (many secondary septa), or absent; all hyphae inamyloid; pigment of the cuticular layer fuscous or sepia, vacuolar, never absent; stipe central, usually white or mouse gray, insititious or with a few white scattered fibrils of a scanty basal mycelium; veil none; on wood and stems of *Cormophyta* (often on *Cyathea*, coniferous or dicotyledonous wood).

**Development of the carpophores:** Unknown.

**Area:** Tropical America (but adventitious everywhere in greenhouses).

**Limits:** The limits are clearly indicated in the key characters. If *Pseudohiatula* were erroneously run through the Myceneae key it would most probably be mistaken for

*Hydropus*. However, the structure of the hymenophore is a dependable character when it comes to distinguishing the two genera; furthermore, few species in *Hydropus* have subfree to narrowly adnexed lamellae; practically none have a continuous hymeniform epicutis with conspicuous dermatocystidia; few have scanty basal mycelium; and none has all these characters at the same time. If *Pseudohiatula* should, mistakenly, be looked for in the Marasmieae, it would evidently key out with *Marasmius*; but *Pseudohiatula* is quite different from *Marasmius* sect. *Alliacei* and sect. *Epiphylli*, however, here again, the structure of the hymenophoral trama is constantly different in the two genera.

*State of knowledge:* Four species are now sufficiently known to warrant their definite recognition as belonging in *Pseudohiatula*.

*Practical importance:* Unknown.

## SPECIES

*P. guzmaniana* Sing.; *P. irrorata* (Pat.) Sing.; *P. dorotheae* (Berk.) Dennis apud Sing. [*P. cyatheae* (Sing.) Sing.]; *P. haedinopsis* Sing.

### 112. CYPTOTRAMA Sing.

*Lilloa* 30: 375. 1960.

*Type species:* *C. macrobasidium* Sing.

*Syn.:* *Xerulina* Sing., *Sydowia* 15: 59. 1961 (published 1962).

*Characters:* Habit of the carpophores collybioid; pileus non-viscid, subglabrous to pubescent under a lens, or distinctly furfuraceous-floccose with often pyramidal connivent surface hyphae which may or may not originate in a hymeniform or sub-hymeniform basal layer, but form a trichodermial palisade; if, however, this ornamentation (also present on the stipe surface) is absent, the epicutis is clearly sub-hymeniform or hymeniform in all cases; dermatocystidia thick- or thin-walled, not considerably projecting beyond the hymeniform layer in the subglabrous forms; hypodermium non-gelatinized or subgelatinous, more rarely distinctly gelatinized (but then the pigment of the pileus spadiceous or brown, vacuolar in KOH); lamellae usually adnate (sometimes appearing decurrent in dried material), subdistant or distant, white or colored; spore print white; spores hyaline, ellipsoid, ventricose, cylindric, or subglobose, smooth with homogeneous, inamyloid, acyanophilic wall, medium sized ( $> 4.5 \mu\text{m}$  long) or large (reaching as long as  $16 \mu\text{m}$ ); basidia normal, most frequently 4-spored, without siderophilous granulation; basidioles not or not consistently fusoid; cystidia or pseudocystidia, or sometimes metuloids, frequently present; trama monomitic, but the lateral stratum of the hymenophoral trama sometimes gelatinized, especially near the edge-end of the lamellae; hymenophoral trama bilateral; clamp connections present or absent; all hyphae inamyloid; pigment

of the cuticular layer of the pileus and stipe intracellular as well as (frequently) intraparietal, on cystidia and dermatocystidia often incrusting, in other species only vacuolar rarely absent; colors: fuscous-sepia, ochraceous, orange-rufescent, bright yellow, olive, or reaching "burnt sienna" M & P or lateritious; stipe central, usually either white or colored like the pileus (at least in the lower portion), insititious or with distinct basal mycelium; veil none; on all kinds of wood.

*Development of the carpophores:* Hemiangiocarpous (primordia of the flocculose species have the aspect of a minute echinate *Lycoperdon* with small, elongate sterile base), at least in section *Xerulina*.

*Area:* Mainly in the tropics and subtropics (neo- and paleotropics), but in America reaching the temperate zone both in the Northern and the Southern Hemisphere; not known from Europe or Northern Asia, but present in Australia, extratropical East Asia and Oceania.

*Limits:* This genus is easily recognizable within the tribus if the key characters are used, and the descriptions of the genera are carefully compared. Before the importance of the structure of the hymenophoral trama was fully appreciated, the species with floccose pileus and stipe were thought to be related to *Oudemansiella*; it was noticed later on that moreover the floccose particles consisted of prolongations (in the form of septate hyphae forming a palisade or fascicles) of sterile elements in an originally well differentiated subhymeniform or hymeniform layer of short elements which are not unlike those of *Oudemansiella*. Nevertheless, aside from the structure of the hymenophoral trama, there are also other characters by which the species of *Cryptotrama* can be distinguished from *Oudemansiella*, particularly the non-radicant stipe and acyanophilic spores. Whether the pileus is flocculose or subglabrous-pubescent is merely a function of the degree of proliferation of the sterile elements of the epicutis, and consequently, it turned out, after enough species had been studied, that *Xerulina* is too closely related to *Cryptotrama* to be kept in a different genus. Aside from *Oudemansiella*, the genera *Physocystidium* and *Hydropus* can also be confused with *Cryptotrama* if the structure of the hymenophoral trama is wrongly interpreted or neglected. *Physocystidium*, however, with its lack of gelatinized tramal portions, intraparietal and incrusting pigment, and close lamellae as correlated characters, differs from *Cryptotrama* by a comfortably broad hiatus. *Hydropus* is the genus which, among the Myceneae at least, comes closest to *Cryptotrama* if the structure of the hymenophoral trama is neglected. However, in all doubtful cases, i.e. where the spores are inamyloid and the pigments are within the range of colors known to occur in *Hydropus*, or in species without clamp connections, the habit of the carpophores is different in the two genera, being much more definitely omphaloid, if *Hydropus* is the appropriate genus. If the trama of the pileus is at all gelatinized, it is in *Hydropus* where we find it gelatinized in its lower portion (just above the lamellae) and in *Cryptotrama* where the gelatinous layer occupies the upper stratum. If the pseudo-cystidia contain an oily emulsion, optically visible as differentiated contents or if they resemble coscinocystidia, the species belonging to *Cryptotrama* has characteristically long ( $> 10 \mu\text{m}$ ) and narrow ( $Q = 2.5-3$ ) spores.

*State of knowledge:* The genus, as restudied recently, contains eleven species definitely belonging in it (combining the species of *Xerulina* and *Cryptotrama* sensu str.) and studied by this author.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *XERULINA* (Sing.) Sing. 1972. Pileus macroscopically flocculose, flocose, pustulate-furfuraceous, the superficial particles mostly pyramidal, and reappearing on the surface of the stipe; on the latter from dermatocystidia, on the pileus from proliferating dermatocystidia forming a trichodermial palisade or convenient fascicles; hymeniform or subhymeniform epicutis not exposed but visible only in sections of the cuticular layer, not persistent.

*Type species:* *Xerula chrysopepla* (Berk. & Curt.) Sing.

*C. aspratum* (Berk.) Redhead & Ginns (*C. chrysopeplum* (Berk. & Curt.) Sing.; *Xerulina*, Sing.; *Xerula*, Sing.; *Lentinus*, Berk. & Curt.; *Collybia* Pearson; *Omphalia scabriuscula* (Peck) Sacc.; *Tricholoma lacunosum* (Peck) Sacc.; *Collybia*, Peck 1891; *Marasmius aculeatus* Pat.; *Lepiota aurantiogemmata* Charles & Burl.; *Pleurotus aureotomentosus* Kalchbr.); *C. lachnocephalum* (Pat.) Sing.; *C. verruculosum* (Sing.) Sing.; *C. costesii* (Speg.) Sing.; evidently also *Marasmius echinatus* Rom. (probably a synonym of *C. costesii*) and *Clitocybe verruculosa* De Seynes (*Xerulina deseynesiana* Pegler).

Sect. 2. *DEPAUPERATUM* Sing. (1977). Pileus flocculose as in sect. 1; spores medium sized ( $5.5-8.5 \times 3.5-5.3 \mu\text{m}$ ); cystidia on sides of lamellae absent; hyphae without clamp connections; stipe subinsititious or with basal mycelium; pigments not red.

*Type and only known species:* *C. depauperatum* Sing.

Sect. 3. *CYPTOTRAMA*. Pileus macroscopically subglabrous, under a lens usually finely pubescent or appressedly fibrillose; clamp connections present; spores either subglobose or over  $10 \mu\text{m}$  long; pileus not bright red nor rusty brown; cystidia and/or pseudocystidia present.

*Type species:* *C. macrobasidium* Sing.

*C. macrobasidium* Sing.; *C. platense* Sing.; *C. dennisii* Sing.; *C. niveum* Sing. (ined.)

Sect. 4. *APORPOTRAMA* Sing. (1972). Pileus as above but bright red or rusty brown; clamp connections absent; spores elongated, more than  $9 \mu\text{m}$  long; cystidia or pleurocystidia present or absent.

*Type species:* *C. hygrocybooides* Sing.

*C. pauperum* Sing. (ined.); *C. hygrocybooides* Sing.

*Mycologia* 73: 506. 1981.

*Type species: C. violascens* Sing.

**Characters:** Habit of carpophores collybioid to pluteoid, pileus and stipe velutinous or subvelutinous (at least under a lens), often also pruinose or granular or rimulose; cuticular layer of pileus and/or stipe trichodermial with the terminal cells dermatocystidoid and forming a palisade; hypodermium short-celled non-gelatinized; pigments here strongly incrusting the walls, resinous, stramineous or ocher to deep spadiceous, often the incrustation broken off into large chunks and dissolved completely in NH<sub>4</sub>OH and KOH, and thereby turning violet or purplish violet, coloring the cell interior purple or violet; lamellae bux yellow to brownish, varying brown or olive, attenuate-free to adnexed, close to subdistant; spores minute (up to 4.5 × 3.8 µm), smooth, in water (taken from spore print) hyaline, tending to become violet from the dissolving pigments of parts of the carpophore in NH<sub>4</sub>OH and KOH mounts, but a small minority of spores often with an ocher to deep spadiceous resinous incrustation, and/or partly purple (dissolved or granular, solid intracellular pigment), acyanophilous (but the pigmented ones cyanophilous), inamyloid, with thin (if incrusted moderately thickish) homogeneous wall, ovate to ellipsoid or short-ellipsoid, a few subangular, often sticking together in tetrads; basidia normal (neither of the *Hygrophorus* nor of the *Lyophyllum* type), 4-spored. Cheilocystidia and frequently also cystidia numerous; hyphae inamyloid, with clamp connections; hymenophoral trama bilateral (*Phylloporus* type); eventually regular or subregular, of filamentous but often swollen (to ± 12 µm) hyphae; stipe central, not insititious but with sparse to ample sordid pallid to deep brown basal mycelium; context unchanging on exposure, inodorous. On earth and on buried rotten chips of wood.

**Development of the carpophores:** Unknown.

**Area:** Amazonas region, perhaps pantropical.

**Limits:** The characteristic violet or purple solution of the pigments in alcaline media is and the small spores are very characteristic even if the bilateral hymenophoral trama is not evident any more in adult material. If the internally colored spores in some collections suggest *Callistosporium*, it should be remembered that the latter lacks clamp connections. The closest relative is undoubtedly *Cryptotrama*, but there the pigments are different, the spores somewhat to much larger. The only species - unknown to me but described by Pegler (*Kew. Bull. Add. ser. 6: 155. 1977*) - showing somewhat intermediate characters - is *Xerulina deseynesiana* Pegler (*Clitocybe verruculosa* De Seynes). The white basal mycelium on a swollen base, the furfuraceous scales of the pileus and the slightly larger spores of this species suggest *Cryptotrama* and the pigments are not described in a way suggesting *Callistodermatum*.

**State of knowledge:** Only one species has been described thus far, but a variety with olive colored lamellae and one with the pigments turning purple instead of violet have been observed in Amazonia. Further observations are indicated as to whether these are strictly related microspecies or forms.

**Practical importance:** Unknown.

# SPECIES

*C. violascens* Sing.

## Tribus *Rhodoteae* Imai

*Journ. Imp. Univ. Hokk.* 1: 237. 1938.

Type genus: *Rhodotus* Maire.

**Characters:** Hymenophoral trama slightly but distinctly bilateral; spore print light pink; spores rough, uni-nucleate; cyanophilic. Carpophores somewhat pleurotoid (with eccentric stipe) and growing on wood; epicutis not a cutis; basidia not of the *Lyophyllum*- or *Hygrophorus*-type. Only the type genus is known.

### 114. RHODOTUS R. Maire

*Bull. Soc. Myc. Fr.* 40: 308. 1925.

Type species: *Rhodotus palmatus* (Bull. ex Fr.) R. Maire.

**Characters:** Habit pluteoid-pleurotoid; pileus with an epicutis of erect vesiculose or ampullaceous thick-walled bodies which are pedicellate, the pedicels reaching downward into a gelatinized zone; lamellae free to subfree; spore print creamy pink; spores stramineous, hyaline, subglobose, finely echinulate-rough, with moderately thin wall, inamyloid, the wall homogeneous (as far as can be established considering the small size of the spores and especially the ornamentation), cyanophilic; cystidia usually none, not even at the edge of the lamellae; hymenophoral trama distinctly bilateral when young, later less distinctly so; stipe almost central to eccentric; veil and pseudorrhiza none, context hygrophanous and often watersoaked but gelatinous mainly in the immediate neighborhood of the hypodermium of the pileus, consisting of inamyloid tissue; all hyphae with clamp connections. On dead frondose wood.

**Development of the carpophores:** Paravelangiocarpous (cf. G. Doguet (1956)); stipitocarpous or slightly pileostipitocarpous.

**Area:** Europe, North Africa, Caucasus, North America; probably circumpolar.

**Limits:** The genus cannot be confused with others, nor its tribus with other tribus of the Tricholomataceae. It has formerly been inserted in the family Amanitaceae but is obviously closer to tribus Pseudohiatuleae of the Tricholomataceae.

**State of knowledge:** The only species is well known.

**Practical importance:** None.

## SPECIES

*R. palmatus* (Bull. ex Fr.) R. Maire (Crepidotus, Gillet; Gymnopilus, Karst.; Pleurotus, Quél.; Gyrophila, Quél. 1888; Agaricus subpalmatus Fr.; Pleurotus, Gillet).

## AMANITACEAE Roze

*Bull. Soc. Bot. Fr.* 23: 51. 1876 (ut Amanitées, nom. nud.); *l.c.*, p. 114; Heim, *Treb. Mus. Ciènc. Nat. Barcelona* 15(3): 111. 1934.\*

Type genus: *Amanita* Pers. ex S.F. Gray.

**Characters:** Habit pluteoid, i.e. fleshy in pileus and stipe and with free or subfree lamellae; lamellae mostly medium broad to broad, thin, lamellulae often truncate; volva absent or present, not always well developed at the base of the stipe, but in some species reduced to a glutinous sheath, a band along the margin of the margined bulb, or simply a sequence of floccons, mealy matter, banded ring-zones etc., but in this case leaving volval patches, volval floccons, or volval pustules on the surface of the pileus; annulus superus present, more rarely absent; an additional median veil sometimes present; hymenophoral trama bilateral in the mature lamellae, regular or bilateral in the primordia, hyphae of the lateral trama tending to be broadened or clavate; trama of the pileus and stipe monomitic, fleshy, terminal hyphal cells often strongly inflated to spherocystoid (*Amanita*-structure), inamyloid, with or without clamp connections; basidia normal, i.e. without siderophilous granulation and not excessively long in most cases, 2-spored, or 4-spored; cystidia generally none, but vesiculose floccons adhering to the edge of the lamellae in most species (these vesiculose cells may be termed free cheilocystidia); spores varying from globose to cylindric, mostly short-ellipsoid to subglobose, smooth with homogeneous thin wall, rarely with a slight punctuation, amyloid or inamyloid, acyanophilic, binucleate. Mostly on earth or humus in wooded areas and frequently obligatorily ectotrophically mycorrhizal. - Development of the carpophores "hemiangiocarpous" (bivelangiocarpous and pileocarpous); hilum of spores of the nodolose type.

Type genus: *Amanita* Pers. ex Hooker.

**Limits:** A small modification has been made in the delimitation of this family as compared with the two first editions. The genera with inverse hymenophoral trama have been separated on the family level rather than as tribus of the Amanitaceae. This has been done following a survey of the cyanophily of the spore walls which showed strongly and distinctly cyanophilic spores in the Pluteaceae (*Pluteus*, *Chamaeota*, *Volvariella*) whereas *Amanita* and *Limacella* have absolutely or virtually acyanophilic spores. Furthermore, *Termitomyces* has been transferred to the Tricholomataceae since it is obvious that the main character common to it and

\*According to the Sydney rules the family Amanitaceae is illegitimate.

*Amanita*, the bilateral trama of the hymenophore, is not valid since the frequently somewhat persistent bilaterality of some species of *Termitomyces* is anatomically and embryologically not comparable to that of the genus *Amanita*. The same is true for *Rhodotus* - a genus whose isolation has always been stressed which has more persistent bilaterality, also of a different type, and is now transferred to the Tricholomataceae likewise.

The family Amanitaceae is thus much more clearly defined and there should be no difficulties in its delimitation.

#### KEY TO THE GENERA

- A. Pileus not or slightly viscid; volva more or less developed, often as scabrosities or patches on the surface of the pileus; annulus (superus) present or absent; hymenophoral trama of the primordia regular; spores amyloid (and then margin of the pileus usually smooth) or inamyloid (and then margin of the pileus usually sulcate striate, or pectinate); stipe not viscid or glutinous; frequently ectomycorrhizal. 115. *Amanita*, p. 443
- A. Pileus slightly viscid or glutinous; volva none or entirely slimy-glutinous; hymenophoral trama of the primordia of divergent hyphae; spores inamyloid and no correlation between the striation of the margin and the amyloidity of the spores existent; stipe often glutinous or viscid; not obligatorily ectomycorrhizal. 116. *Limacella*, p. 453

#### 115. AMANITA Pers. ex Hooker

*Flora Scot.*, 2: 19, May 1821 non *Amanita* Dill. ex Boehmer (1760).

*Type species: A. muscaria* (L. ex Fr.) Hooker.

- Syn.: *Agaricus*, trib. *Amanita* (Pers. ex) Fr., *Syst. Mycol.* 1: 12. 1821.  
*Vaginata*, Nees ex Gray, *Nat. Arr. Brit. Pl.* 1: 601. 1821.  
*Amanitopsis* Roze, *Bull. Soc. Bot. Fr.* 23: 51. 1876.\*  
*Pseudofarinaceus* O. Kuntze, *Rev. Gen. Pl.* 2: 867. 1891.  
*Venenarius* Earle, *Bull. N. Y. Bot. Gard.* 5: 450. 1909.  
*Leucomyces* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 451. 1909.  
*Amanitella* Earle, *Bull. N. Y. Bot. Gard.* 5: 449. 1909.  
*Lepidella* Gilbert, *Bull. Soc. Myc. Fr.* 41: 293. 1925, non Van Tiegh (1911).  
*Aspidella* Gilbert, in Bresadola, *Icon. Mycol.* 27: 63. 1940.  
*Ariella*, Gilbert, *l.c.*, p. 76.  
*Amanitaria* Gilbert, *l.c.*  
*Amidella* Gilbert, *l.c.*, p. 77.  
*Amplariella* Gilbert, *l.c.*, p. 78.  
*Amanitina* Gilbert, *l.c.*  
?Metraria Cooke & Mass. ap. Sacc., *Syll.* 9: 82. 1891 (see also p. 512 and p. 609).

*Characters:* Margin sulcate and then spores inamyloid, or margin smooth or almost so, and the spores amyloid; fragments of an at least rudimentary volva (Pl. 33, 1) (but in many species, volva membranous to fleshy and well developed) present either on the surface of the pileus or/and on the base of the stipe; annulus superus present, or more rarely absent; lamellae alternating with lamellulae which are either

\*Applying the Sydney rules, *Amanitopsis* (nom. conserv.) would be the "correct" name for all Amanitae.

sharply emarginate (as if cut off), or attenuate; lamellae free or almost so (sometimes slightly adnexed but separating in age, decurrent with a tooth which breaks off in age, or with decurrent lines at the apex of the stipe); spore print pure white, cream color, greenish, or pink (rarely so, and then spores amyloid); spores typically over 7.5  $\mu\text{m}$  long, smooth or very densely and minutely verruculose punctulate in one or two species, acyanophilic or almost so, medium sized to large, thin-walled, binucleate according to Kühner, globose to cylindric; basidia rather voluminous, without carminophilous granulosity, 4-spored, rarely constantly 2-spored; cystidia none, but cheilocystidia or pseudocystidia rarely present; the latter, however, are hardly true cystidia nor are they pseudocystidia but rather fragments of the annulus superus that adhere to the edge of the lamellae when the pileus expands; hymenophoral trama bilateral with rather broad elements; stipe central; bulb at its base present or absent; context fleshy, changing or unchanging when bruised, consisting of a tissue of special structure (*Amanita*-structure, see p. 111), inamyloid; hyphae with or more frequently without clamp connections. On the ground very rarely on other substrata, not growing from a pseudorhiza that is inserted in termite nests, usually in the forests, all except some species of the section *Lepidella* obligatorily ectomycorrhizal.

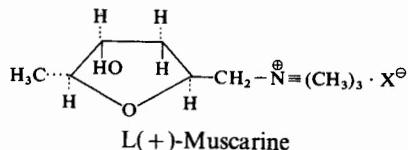
*Development of the carpophores:* Bivelangiocarpous and pileocarpous, with (in the primordia) regular hymenophoral trama, according to Reijnders.

*Area:* Almost cosmopolitan (not in the Antarctic), but the species themselves occupying definite smaller areas.

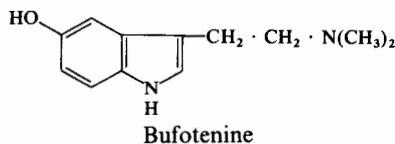
*Limits:* The delimitation of this genus as accepted in the present work is adequately expressed in the key, and is not in need of further elaboration. The author, like many other taxonomists, recognized the genus *Amanitopsis* as an autonomous genus, in his classification of 1936. However, the discovery of numerous African species in the Congo region by Beeli, Gilbert, and Heim throws a different light at this problem. The final proof for the generic identity of *Amanitopsis* with *Amanita* is a specimen of *A. fulva*, found near Mountain Lake, Virginia, U.S.A. by the author in 1946. It differs from other specimens of the same species, also collected nearby, in having a distinct, well developed annulus superus, exactly as *Amanita caesarea*, or *A. muscaria*. This specimen emerged from rather heavy gravelly soil, and it is possible that a higher pressure during the development of the primordia may cause annulate forms. Whatever the reason, it is now obvious that the annulate or non-annulate character of the *Amanitae* is not a generic character, and under certain circumstances not even a specific character.

*State of knowledge:* Numerous monographs of a regional character, covering particularly Europe, North America, tropical Africa and North Africa as well as Eastern and tropical Asia, Australia, parts of South America, have made this genus relatively well known and Gilbert (1940-41) has added interesting data and illustrations on the species described until then. A formal world monograph is available (Bas 1969) only for one of the sections (*Lepidella*), and here I have followed Bas, including also the delimitation of *Lepidella* (which in Bas' treatment contains all Amanitas with amyloid spores). More use of such characters as clamp connections and color reactions will help monographing the other sections. We enumerate 100 species.

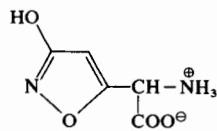
*Practical importance:* *Amanita muscaria* has in the past been used for medicinal purposes and as hallucinogenic mushroom, particularly the Eastern Asiatic var. *kamtschatica*, possibly an independent species (*A. caesareaoides* Vassilieva?) in Northeastern Asia. This employment may have been much more widespread many years ago. The species is also poisonous when used in large quantities (especially in the Northeastern race in America - ssp. *americana*, which is often confused with *A. caesarea*). A decoction in milk with sugar added, is used (and was probably widely used in former times) to kill - or rather paralyze - flies, e.g. in Northern Russia where I have applied the method successfully myself. Dried *A. muscaria* - mostly for purposes of intoxication - has been traded extensively in historic times, especially in Northeast Asia. The physiologically and psychotropically active substances isolated from *A. muscaria* are the alkaloids muscarine and bufotenine, muscimol and ibotenic acid. The first of these, present only in small amounts, was first isolated by Kögl, Duisberg and H. Esleben, restudied and the formula corrected by Eugster & Waser and again revised by Kögl & al. (1957):



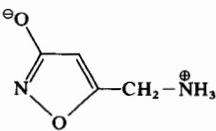
Bufotenine was chromatographically shown to be present in some race or variety of *A. muscaria* but its presence was denied by other biochemists; however, it must be taken into consideration that the relative concentration and perhaps even presence or absence of these alkaloids is different in different races, and perhaps even within them. The physiological and psychotropic action is probably due to a mixture of several active substances.



Muscimol and ibotenic acid are apparently the fly-killing agents in this mushroom.



Ibotenic acid



Muscimol

Other substances isolated from *A. muscaria* are acetylcholine, muscazone and other unidentified indol-bases (Wieland 1968).

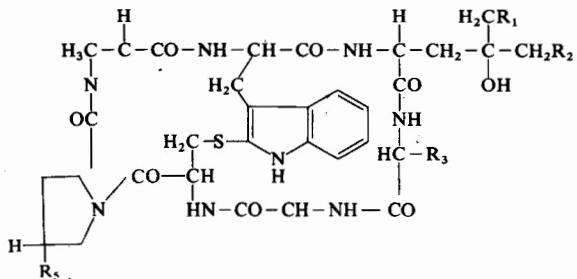
As for other species containing alkaloids, it has been shown that bufotenine exists in carpophores of *A. citrina* and *A. porphyria*. An alkaloid was also found to be present in *A. gemmata*, at least in the race which caused deadly poisonings in Chile in 1967. The case of *A. gemmata*, such as occurring in pine plantations adventitiously, is quite interesting since few well documented poisonings have been related from its native habitats in Europe and North America. The Chilean material has been identified by me (1969).

Other species of *Amanita* with alkaloids causing poisonings are *A. pantherina* (containing, according to Wieland, among several alkaloids, ibotenic acid) and apparently *A. bingensis* (Beeli) Heim, *A. citrina* and *A. porphyria* (the latter two with amyloid spores, i.e. belonging in a group where another type of poisonous substances is very important: the amanita-toxins); obviously also some species of the section *Lepidella*, cf. *A. strobiliformis*.

Amanita-toxins are complex cyclopeptides which were found or isolated in the most dangerous and mortal poisonous fungi - *Amanita phalloides*, *A. bisporigera*, *A. tenuifolia* Murr. (perhaps identical with *A. bisporigera*), *A. verna* (= *A. virosa*), and other species identified as, but not identical with *A. verna* such as *A. ocreata* Peck. Formerly all species of this group, including *A. citrina*, *A. brunneascens* and *A. aestivalis* were considered equally poisonous as *A. phalloides* but recent chemotaxonomic studies do not bear out this contention although it is certainly justified to warn the amateur against eating any or all species belonging in the so-called Phalloides-group (sections 5-7).

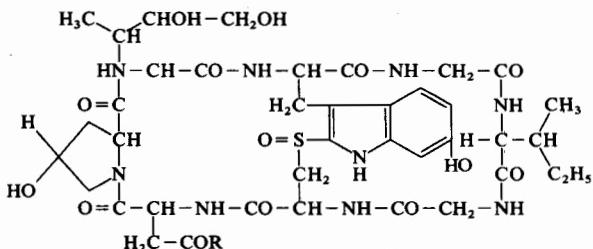
The Amanita-toxins have been studied by Wieland whose summary (*Science* 159: 946-952, 1968) is very instructive for the chemotaxonomist and toxicologist as well as the mycophagist. The Amanita-toxins have a molecular weight of about 1000, containing sulphur, and are divided into two categories (a third, virotoxins, is less common).

(a) phallotoxins which are of quick (physiological) action and (b) amatoxins which are of characteristically slow action. The former group consists of at least five defined members. Their common cyclic heptapeptide skeleton is



Phallotoxins (R = radical)

The amatoxins consist of at least six members, two of them particularly important viz.  $\alpha$ -amanitin and  $\beta$ -amanitin with the following formula, whereby the radical R is NH<sub>2</sub> in  $\alpha$ -amanitin, and OH in  $\beta$ -amanitin:



It is curious to note that muscarin occurs aside from the fly mushroom also in several unrelated agarics; a close derivative of ibotenic acid - tricholomic acid - has been obtained from *Tricholoma muscarium* Kawamura which is said to have insecticidal properties. Similarly  $\alpha$ - and  $\beta$ -amanitin occur likewise in three poisonous species of *Galerina* (Cortinariaceae), *Phaliotina* (Bolbitiaceae) and in *Lepiota*.

The first point of attack in the human organism is, as far as the amanitins are concerned, the gastrointestinal mucous membrane; but microlesions and later liver damage will eventually lead to hepatic necrosis. A complete understanding of the mechanism of *Amanita phalloides* poisoning on a molecular basis has not yet been achieved. Wieland expects that such an insight would also be of general interest in cell physiology. It would also explain why extracts of *Amanita phalloides* have given very encouraging results with the treatment of cancer tumors in Argentina.

Species which have been indicated as poisonous without any indication of the chemical composition of the toxic substances involved are: *A. agglutinata*, *A. chlorinosma*, *A. vittadinii*, *A. tainaomby*.

The best known treatment is thioctic acid ( $\alpha$ -lipoic acid) in massive doses and as early as possible, as far as amanitatoxins are involved (Kubička 1964, 1968, 1969). Physicians treating poisonings with amanitatoxins should be fully acquainted with Kubička's papers\*. Dr. Bastien's procedure is also said to have been successful (cf. Monthoux, *Schweiz. Zeitschr. f. Pilzk.* 60: 194-203. 1982). Recently silybin in combination with penicillin has shown to give good results (Flammer, *Differentialdiagnosen der Pilzvergiftungen*, G. Fischer 1980, p. 17; Flammer & Horak, *Giftpilze, Pilzgifte*, 1983, p. 26; Hruby, Csomas & Thaler ined. 1985; Bresinsky-Besl, 1985, p. 23).

Floersheim (1972) who had formerly stated that some allegedly useful substances such as thioctic acid, glucocorticosteroids and coenzyme A did not counteract - unless given simultaneously with amanitatoxin - the lethal poisoning with  $\alpha$ -amanitin (*Schweiz. Med. Woch.* 102: 901. 1972) under controlled conditions, has recently indicated that this toxin which he considers the one mainly responsible for the clinical mortality, can be controlled in mice even after 8 hours by administering cytochrome c and penicillin-G at the same time, providing antidotal effects with a survival of 62% (*Science* 177: 808. 1972). No clinical data about human reaction has been re-

\*especially Kubička, J., J. Veselský & R. Čurík, Muchomorka zelená (*Amanita phalloides*) - klinické otravy a léčebné postupy (*Amanita phalloides* - Clinical pictures of intoxication and therapeutic techniques). *Čas. Lék. Čes.* 117(8): 245-249. 1978.

ported, either with Floersheim's combination nor with Wieland's et al. (1968) antamanid.

Several recent papers indicate that elevated doses of  $\alpha$ -amanitin act by binding to RNA polymerase in eukaryotic cells and inhibiting this enzyme. Because of this property, the toxin has been adopted as a tool in molecular biochemical research (Floersheim).

Muscimol (from *A. muscaria*) is also interesting for practical purposes because of its possible use in food fermentation since it is a strong flavoring agent (twenty times more intense than sodium glutamate) according to Wieland (1968).

On the other hand, there are also many Amanitas which are good edible mushrooms and have been used and sold as such since antiquity. The original boletus of the Romans was not a boletaceous mushroom but *A. caesarea*. *A. ovoidea* was also known in the Mediterranean region since antiquity. *A. rubescens* is often indicated as being especially in demand in England. Several other species may be eaten not only with impunity but are rightly classified among the most delicious mushrooms.

Some species of *Amanita* contain antibiotic substances. Many will also become important in forestry since they are important ectomycorrhizal fungi; their host range is often wide which favors forestation with foreign mycorrhizal trees in regions where other mycorrhizal trees grow naturally. However, many species of section *Lepidella* appear to be non-mycorrhizal. This is certainly so in the case of *A. nauseosa* which grows in Mexico as well as in Brazil in fully anectrotrophic forests and in England in greenhouses.

The old controversy (Paulet versus Ascherson) - whether a given fungus species can be, according to habitat or geography, vary from poisonous to harmless and vice versa - seems to be decided in favor of Ascherson. Like some other chemical characters, the presence or absence, and certainly the quantity, of poisonous matter such as alkaloids and toxins, is, in the case of *A. gemmata*, and probably other species of *Amanita*, not necessarily hereditary, and apparently sometimes subject to minor mutations.

## SPECIES

Subgenus *Amanita* (*Pseudoamanita* Sing. 1936, 1950; *Vaginaria* Forquignon 1888; *Amanitopsis* (Roze) Barbier). Spores inamyloid; margin striate, sulcate or pectinate; spore print pure white; annulus superus well developed or absent; pigment usually abundant in the pellicle of the pileus, more rarely almost absent; odor never of chloride of lime, not pungent; the poisonous species do not contain cyclopeptides, but alkaloids.

Type species: *A. muscaria* (L. ex Fr.) Pers. ex S.F. Gray.

Sect. 1. *CAESAREAE* Sing. (1950). Annulus and volva well developed; stipe not or slightly bulbous; volva saccate, neither friable (or rarely so) nor limbate; spores elongate (short ellipsoid, oblong, or cylindric); as far as known no poisonous matter present.

Type species: *A. caesarea* (Scop. ex Fr.) Pers. ex Schw.

*A. cokeriana* Sing. (*A. recutita* sensu Coker non Fr.); *A. spreta* Peck with var. *minor* Beardslee [*A. cinerea* Bres. non (Otto ex Fr.) Secr.; *A. spreta* var. *cinerea* (Bres.) Gilbert; *Venenarius subvirginianus* Murr.]; *A. murrilliana* Sing. (*Venenarius gemmatus* var. *volvatus* Murr.); *A. calyptrotooides* Peck; *A. caesarea* (Scop. ex Fr.) Pers. ex Schw.; *A. hemibapha* (Berk. & Br.) Sacc.; apparently also *A. caesareaoides* Vassilieva; *A. gayana* (Mont.) Sacc., and *A. similis* Boedijn (?*A. jacksonii* Pomerleau); furthermore *A. cinereoannulosa* Cleland; *A. lactea* Malençon, Romagnesi & Reid; *A. annulatovaginata* Beeli; *A. infusca* Gilbert; *A. luteoflava* Beeli; *A. robusta* Beeli; *A. strobilaceovolvata* Beeli.

Sect. 2. *OVIGERAЕ* Sing. As section 1, but completely and consistently without an annulus. Volva saccate, free or marginate or friable.

Type species: *A. biovigera* Sing.

*A. biovigera* Sing.; *A. tainaomby* Heim; *A. calopus* (Beeli) Gilbert; *A. farinosa* Schwein.; perhaps also *A. bingensis* (Beeli) Heim; *A. lanivolva* Bas; *A. coacta* Bas.

Species transitional to sect. 3. (Spores with a Q = 1.1-1.4): *A. humboldtiana* Sing.; *A. nivalis* Grev.; *A. friabilis* (Karst.) Bas; *A. sulcatissima* Bas (*Collybia sulcatissima* Rick?); *A. crebresulcata* Bas; *A. antillana* Dennis; obviously also *A. argentea* Huijsman and *A. obsita* Corner & Bas.

Note: Species with bulb, even if exannulate, are considered to belong in sect. *Amanita* by Bas. In future classifications sections 1-4 will probably be re-arranged.

Sect. 3. *VAGINATAЕ* (Fr.) Quél. (*Amanitopsis* (Roze) Konr. & Maubl.); as section 2, but Q of spores 1-1.1; volva rarely friable, mostly more or less saccate, stipe without a conspicuous basal bulb.

Type species: *A. vaginata* (Bull. ex Fr.) Vitt.

*A. vaginata* (Bull. ex Fr.) Vitt. (and several closely related species, some with, some without clamp connections, until now not well defined); *A. strangulata* (Fr.) Roze apud Karst.; *A. crocea* (Quél. apud Bourdot) Sing.; *A. fulva* (Schaeff. ex) Pers.; *A. inaurata* Secr.

Sect. 4. *AMANITA* (Muscariae (Fr.); *Circumscissae* Quél.; *Amanitaria* (Gilbert) Konrad & Maubl. 1948; *Myoperda* K.F. Schultz ex G. Beck 1922). Annulus sometimes (not consistently in a single species) and volva usually strongly reduced, often appearing as a narrow ring or concentric rings around the bulb of the stipe which is usually rather abrupt and well formed (but not always so), sometimes volva in concentric rows of warts, on the pileus more often in form of small patches, warts or pustules than in broad smooth flakes; spores generally not globose; species frequently containing various alkaloids.

Type species: *A. muscaria* (L. ex Fr.) Pers. ex Hooker.

*A. gemmata* (Fr.) Bertillon (*A. toxicina* (Lazo) G. & B.); *A. diemii* Sing.; *A. cothurnata* Atk.; *A. aurantiovelata* Schalkwijk & Jansen (*A. gayana* (Mont.) Sacc. sensu

\*the last five species are considered subspecies of *A. caesarea* by some authors.

Sing.\*); *A. umbrinella* Gilbert & Cleland; *A. monticulosa* (Berk. & Curt.) Sacc.; *A. muscaria* (L. ex Fr.) Pers. ex Hooker with ssp. *muscaria*, ssp. *americana* (Lange) Sing., ssp. *flavivolvata* Sing. and perhaps var. *kamtschatica* (Langsd. ex Fr.); *A. regalis* (Fr.) Michael; *A. frostiana* (Peck) Sacc.; *A. parcivolvata* (Peck) Gilbert; *A. pantherina* (D.C. ex Fr.) Kummer (non *A. pantherina* Secr.); *A. xerocybe* Bas; perhaps also *A. atra* (Beeli) Sing.

Subgenus **Lepidella** (Gilbert) Vesely (1933) (*Eu-Amanita* Sing. 1936, 1950). Spores amyloid (very rarely inamyloid according to Bas), which character is correlated with smooth margin (margin rarely slightly and short sulcate in age); annulus generally present; volva varying from saccate to strongly reduced, often friable and scarcely visible at the base of the stipe; spore print mostly pure white, more rarely pale cream, salmon or greenish; pigments present or absent; odor often disagreeable or pungent, sometimes of calcium oxychloride.

Type species: *A. vittadinii* (Mor.) Vitt.

Sect. 5. **AMIDELLAE** (Gilbert) Konr. & Maubl. (1948). Spores strongly elongate, ellipsoid to cylindric or subglobose (but then basidia bisporous and lamellae not truncate); pigment usually little; annulus sometimes wanting; context sometimes reddening; lamellulae either truncate or attenuate; volva well formed, cup-shaped, saccate and thick and firm. Obligatorily ectomycorrhizal.

Type species: *A. volvata* (Peck) Martin.

*A. ovoidea* (Bull. ex Fr.) Quél. (*A. alba* Pers. ex Vitt.); *A. cylindrispora* Beardslee; *A. mutabilis* Beardslee (*Venenarius submutabilis* Murr.); *A. volvata* (Peck) Martin [*Amanitopsis*, Sacc.; *A. baccata* (Fr.) Quél. sensu Bres., Gilbert 1926 non 1941, vix Fr.; *A. curtipes* Gilbert; *Amanitopsis volvata* (Peck) Sacc.; *A. peckiana* Kauffm.]; *A. ocreata* Peck [*A. verna* (Bull. ex Fr.) Pers. ex Vitt. sensu Vitt. 1826, Arcangeli, Gilbert, A.H. Smith, Singer 1950, 1951, non Fr. 1821]; *A. bisporigera* Atk.; *A. hygroscopica* Coker. Probably also *A. subviscosa* Beeli, *A. goossensiae* Beeli and *A. duplex* Corner & Bas and *A. magnivelaris* Peck.

Sect. 6. **PHALLOIDEAE** (Fr.) Quél. Spores less strongly elongated, never cylindric; pigment often abundant in the pileus; annulus always well developed; context not reddening; lamellulae abruptly truncate; volva well formed, saccate, membranous. All species contain amanitatoxins and are ectomycorrhizal. Most basidia 4-spored.

Type species: *A. phalloides* (Vaill. ex Fr.) Secr. ex Schummel.

Stirps *Phalloides* (pileus more or less distinctly pigmented - olive or "drab" (Ridgway) - or not pigmented; spores subglobose to short ellipsoid).

*A. phalloides* (Vaill. ex Fr.) Secr. ex Schummel and a similar white species generally determined "*A. verna*"; *A. pseudophorphyria* Hongo; apparently also *A. elephas* Corner & Bas; *A. modesta* Corner & Bas.

\*While recognizing the differences between the fungus described by Montagne and mine, the fairly thorough investigation of the Valdivian agaric flora by us has never produced anything near *A. caesarea* and I must consider the fungus represented by Gay as either extremely rare (or extinct) or else misdescribed in several regards.

*Stirps Verna*. (Pileus pigmented or not; spores globose to short-ellipsoid; KOH reaction yellow).

*A. verna* (Bull. ex Fr.) Pers. ex Vitt. (sensu Fr. 1821 non al.) (*A. virosa* Lam. ex Secr.); apparently also *A. privigna* Corner & Bas and *A. alauda* Corner & Bas.

Sect. 7. *MAPPAE* Gilbert. Spores globose or almost so; pigment often abundant in the pileus; annulus always well developed, often a mediane annulus also developed below the annulus superus; context weakly reddening or almost not reddening, but copper red at least in the damaged exposed portions, worm-holes etc.; volva limbate, i.e. with a narrow "limb" extending from a soft, conspicuous, margined bulb, not saccate-lobed or cup-shaped nor membranous; odor reminding one of raw potatoes.

Type species: *A. citrina* (Schaeff. ex) S.F. Gray.

*Stirps Citrina*. (Tryptamine derivatives present including bufotenine; carpophores usually medium sized and with yellow, stramineous or citrinous or prophyry to fuscous or gray, rarely amethyst violet pigments.)

*A. citrina* (Schaeff. ex) S.F. Gray (*A. mappa* (Batsch ex Lasch) Quél.; *A. phalloides* var. *virescens* Corda in Sturm); *A. porphyria* (*A.* & *S.* ex Fr.) Kummer.

*Stirps Brunnescens*. (Tryptamine derivatives like bufotenine absent from the carpophores which are usually rather large, either without any pigment, or the (fuscous) pigment not uniformly distributed so that the pileus appears radially striped.)

*A. aestivalis* Sing.; *A. brunnescens* Atk.

Sect. 8. *VALIDAE* (Fr.) Quél. (*Incompletae* Schröter in Cohn). Spores ellipsoid (fewer short ellipsoid or cylindric); pileus with obtuse or low volval warts, rarely or eventually without these; cuticle in most species pigmented; volva at the base of the stipe little developed; lamellulae sharply emarginate at a right angle as if they were truncate; context not reddening when exposed to the air but sometimes slowly becoming reddish or copper red in age and in worm holes independently of bruising, sometimes slightly bitter; pigment in the pellicle of the pileus generally abundant, exceptionally scarce; base of stipe with extremely scarce or inconspicuous or fugacious volval development.

Type species: *A. valida* (Fr.) Quél. (= *A. excelsa* or *A. spissa*).

*A. spissa* (Fr.) Kummer; *A. excelsa* (Fr.) Kummer; *A. flavorubescens* Atk.; *A. flavoconia* Atk.; *A. rubescens* (Pers. ex Fr.) S.F. Gray (*Venenarius rubens* (Scop. ex Murr.); *A. franchetii* (Boudier) Fayod (*A. aspera* var. *franchetii* Boud. non *A. aspera* Pers.); *A. campinaranae* Bas; *A. phaea* Bas, and apparently also several species from tropical Asia and Africa.

Sect. 9. *ROANOKEENSES* Sing. ex Sing. (1962) (*Lepidella* aut.). Differing from the preceding sections in appendiculate margin of the pileus, frequently obliquely attenuate lamellulae (few or none truncate), pigment on pileus scarce or none, rarely abundant (and then not with the character combinations of the preceding sections); volva variously developed; spores usually ellipsoid to oblong or cylindrical. This differs from sect. *Amidellae* (which is closest) in either not saccate (and never duplex with pulverulent inner layer) volva or, if the volva is saccate, the context does not

redden when bruised. Whole volva sometimes friable; spores often cream, pale gray, palest pink or with a greenish hue, or pale buff; context not reddening when exposed to the air unless volva very narrow, friable or lacerate-floccose; many or most species not (at least not obligatorily) ectomycorrhizal.

*Type species: A. roanokensis* Coker sensu Sing.

Subsection *Vittadiniae* Bas (1969).

Volva consisting mainly of rows of large, inflated, cylindrical, elongate-fusiform, and slenderly clavate cells, sometimes with a few ellipsoid or vesiculose-subglobose cells, especially at the ends of these rows. Stipe usually cylindrical, rarely with a bulbous base; remnant of volva often scattered on the stipe (according to Bas 1969).

*Type species: A. vittadinii* (Mor.) Vitt.

*A. vittadinii* (Mor.) Vitt.; *A. codinae* (Maire) Sing.; *A. prairiicola* Peck; *A. ameghinii* (Speg.) Sing.; *A. lilloi* Sing.; *A. singeri* Bas; *A. bubalina* Bas; *A. nana* Sing.; *A. praegraveolens* (Murr.) Sing.; *A. nauseosa* (Wakefield); *A. foetens* Sing.; *A. aureofloccosa* Bas; also several other species enumerated by Bas (1969) and unknown to me.

Subsection *Solitariae* Bas (1969) (*Strobiliforminae* Sing. 1943, not validly published). Volva composed of versiform elements; rows of large cylindrical to slenderly clavate cells never dominant; stipe usually with bulbous base and remnants of the volva concentrated towards the base; volva not membranous nor nearly membranous, never forming a limb at the base of the stipe, never forming patches on the surface of the pileus, where the outer layer consists of repent hyphae.

*Type species: A. solitaria* (Bull. ex Fr.) Mérat.

*A. cokeri* (Gilbert & Kühner) Gilbert; *A. solitaria* (Bull. ex Fr.) Mérat; *A. ravenelii* (Berk. & Curt.) Sacc.; *A. crassa* Bas; *A. rhopalopus* Bas (*A. radicata* Peck non Vogl.); *A. atkinsoniana* Coker; *A. abrupta* Peck; *A. polypyramis* (Berk. & Curt.) Sacc.; *A. baccata* (Fr.) Gill. (sensu Bas; *A. boudieri* Barla); *A. daucipes* (Mont.) Lloyd; *A. chlorinosma* (Peck apud Austin) Lloyd; *A. cinereoconia* Atk.; *A. subsolitaria* (Murr.) Murr.; *A. solitariiformis* (Murr.) Murr.; *A. rhoadsii* (Murr.) Murr.; *A. strobiliformis* (Paulet ex Vitt.) Bertillon in Dechambre and several other species described by Bas (1969).

Subsect. *Limbatulae* Bas (1969) (sect. *Roanokenses* Sing. ex Sing. 1962). At least the outer layer of the volva consisting mainly of hyphous elements, hence the volva membranous; volva forming at the base of the stipe a slight, sometimes torn limb, or volva circumscissile and bulb distinctly margined. Lamellae not ochraceous.

*Type species: A. limbatula* Bas.

*A. praelongispora* (Murr.) Murr.; *A. roanokensis* Coker; *A. alliacea* (Murr.) Murr., *A. inodora* (Murr.) Bas; obviously also *A. limbatula* Bas and several other species unknown to me.

Subsection *Gymnopodae* Bas (1969). Much like the preceding subsection, but the

volva leaving the base of the stipe (which is not margined) glabrous, rarely forming a small limb there; lamellae ochraceous.

*Type species: A. gymnopus* Corner & Bas.

Neither the type species nor the second species (*A. ochrophylla* (Cooke) Cleland) has been studied by me.

## 116. LIMACELLA Earle

*Bull. N.Y. Bot. Gard.* 5: 447. 1909.

*Type species: Agaricus delicatus* Fr.

*Syn.: Amanitella* R. Maire, *Ann. Mycol.* 11: 357. 1913.

*Amanita* subgenus *Lepiotopsis* Lange, *Dansk Bot. Ark.* 2: 6. 1915.

*Myxoderma* Fayod ex Kühner (1926), Singer (1936).\*

*Amanita* subgenus *Limacella* (Earle) Gilbert, *Le Genre Amanita* Pers., p. 174. 1918.

*Character:* Pileus more or less viscid, without fragments of a volva; epicutis consisting of variously transformed or unchanged terminal members of hyphae which are repent or ascendant or erect in a gelatinous mass; lamellae free or nearly so; lamellulae not truncate (i.e. not abruptly emarginate); spore print white; spores small, more rarely medium sized, smooth or very finely roughened to subpunctulate, hyaline, with homogeneous wall, ovoid or short-ellipsoid, or else ellipsoid to subglobose or globose, inamyloid, sometimes a few spores somewhat pseudoamyloid, acyanophilic; basidia normal; cystidia none; aborted basidioles (pseudoparaphyses) often found on the edges; subhymenium cellular; hymenophoral trama distinctly bilateral when young, later becoming more or less irregular or intermixed; stipe dry or viscid, with a glutinous belt or cortinoid, fleshy, or membranous annulus, but without a membranous-fleshy, or pulverulent volva, always central; context fleshy; tissue inamyloid; hyphae with clamp connections. On the ground, more rarely on decayed wood.

Not obligatorily ectotrophic, at least the majority of species; some may be facultative ectotroph-formers.

*Development of the carpophores:* Bivelangiocarpous in *L. guttata* and *L. glioderma*; pileocarpous in *L. guttata*, less distinctly so in *L. glioderma*.

*Area:* Probably almost cosmopolitan, but most species known from North America.

*Limits:* The differences between *Amanita* and *Limacella* are sufficiently expressed in the key. If the bilateral hymenophoral trama - which is more like that of *Amanita* than of the Tricholomataceae or the families around the Boletaceae - is disregarded, this genus may be confused with *Hygrophorus*, *Oudemansiella*, *Flammulina*, and perhaps *Termitomyces*. The white spore print and non-siderophilous basidia ex-

\*This genus is not actually validly published since it is an alternative for a genus previously published by Patouillard and accepted by Fayod; it does not matter that Fayod's interpretation of Patouillard's genus was erroneous.

clude *Termitomyces*; and the free lamellae the other genera. *Hygrophorus*, in addition, has relatively longer basidia and is ectotrophically mycorrhizal; *Oudemansiella* has larger spores and a different structure of the epicutis; *Flammulina* has dermatocystidia of a very characteristic kind, more collybioid habit, and a different type of spores although the latter are binucleate as they are in *Limacella*.

*State of knowledge:* 15 well known species are here recognized.

*Practical importance:* Some species are edible but they are rarely available in large quantity and have no economic importance.

## SPECIES

Sect. 1. *LUBRICAE* H.V. Smith (1945, nom. nud.). Stipe viscid or glutinous.

*Type species:* *L. illinita* (Fr.) Murr.

*L. glischra* (Morgan) Murr.; *L. kauffmanii* H.V. Smith; *L. floridana* (Murr.) H.V. Smith (Armillaria, Murr.); *L. oblita* (Peck) Murr.; *L. illinita* (Fr.) Murr. (Lepiota, Quél.; Amanitella, R. Maire; Amanita, Gilbert; Myxoderma, Kühner) with the varieties var. *rubescens* H.V. Smith and var. *argillacea* (Fr.) H.V. Smith; *L. roseo-cremea* Murr.; *L. oaxacana* Sing.; *L. alachuana* (Murr.) Sing. (Melanoleuca alachuana Murr., Mycologia 30: 365. 1938).

Sect. 2. *LIMACELLA*. Stipe dry.

*Type species:* *L. delicata* (Fr.) Earle ex H.V. Smith.

*L. roseola* Muir.; *L. guttata* (Fr.) Konrad & Maubl. (Lepiota, Quél.; Agaricus lenticularis Lasch; Lepiota, Gillet; Amanitella, R. Maire; Amanita, Lange; Limacella, R. Maire; Agaricus lerchei Weinmann) with var. *fischeri* (Kauffm.) Sing. (Lepita fischeri Kauffman); *L. solidipes* (Peck) H.V. Smith; *L. glioderma* (Fr.) R. Maire (Lepiota, Gillet; Armillaria, Quél.; Amanita, Gilbert; Amanitella, R. Maire; Melanoleuca subpessundata Murr.; Limacella, Sing.; Melanoleuca subvelata Murr.; Armillaria graveolens Murr.); *L. delicata* (Fr.) Earle ex H.V. Smith (Lepiota, Kummer; Armillaria, Boudier; Amanita, Gilbert); *L. furnacea* (Let.) Maire [L. *megalopoda* (Bres.) R. Maire]; *L. arida* (Fr.) Konr. & Maubl. - According to Konrad & Maublanc and other French authors also *L. persoonii* (Fr.) Konr. & Maubl. but its hymenophoral trama has not been studied.

## PLUTEACEAE Roze

*Bull. Soc. Mycol. Fr.* 23: 51 (nom. nud.); 111. 1876 ("Plutéinées"); Kotlaba & Pouzar, *Ceská Mykologie* 26: 218. 1972.

*Syn.:* *Amanitaceae* trib. *Pluteeae* (Fayod) Maire, *Publ. Junta Ciènc. Nat., Barcelona* 1933, p. 89. 1933; "Plutéidés" Fayod.

*Agaricaceae* subfam. *Volvarioideae* Imai, *Journ. Fac. Agr. Hokkaido Imp. Univ.* 43: 153. 1938.  
*Volvariaceae* Roze, *Bull. Soc. Bot. Fr.* 23: 51 (nom. nud.); p. 111. 1876 (Volvariées); Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 13. 1927.

*Type genus: Pluteus* Fr.

**Characters:** Hymenophoral trama inverse; spore print pinkish, sordid pink, or brownish pink ("cinnamon pink", "Mexico", "saona", "copper lustre", "Paloma", "sonora", "blush", 4-F-9, 12-A/B-8); spores cyanophilic, inamyloid; volva (*Volvariella*) or annulus (*Chamaeota*, p. 457) present, or both absent (*Pluteus*, p. 458); on the soil inside or outside the woods, rarely parasitic on other fungi, frequently on all kinds of wood or litter; never ectomycorrhizal. Otherwise similar to Amanitaceae and Entolomataceae, differing from the former in inverse (although likewise originally regular) hymenophoral trama, more complex spore wall structure, and other characteristics, from the latter mainly in inverse hymenophoral trama and spore shape. Since the suggested orders "Pluteales" and "Agaricales sensu stricto" are principally separated from each other by the spore characters, especially the EM structure of the walls, it would be useful for those tempted to do likewise to study carefully Capellano's results as illustrated and discussed by Kühner (1978, p. 152-153).

KEY TO THE GENERA

- A. A well developed volva present. 117. *Volvariella*, p. 455
- A. Volva none, or indistinct (and then apically horn-bearing metuloids present).
  - B. Annulus present. 118. *Chamaeota*, p. 457
  - B. Annulus absent. 119. *Pluteus*, p. 458

117. **VOLVARIELLA** Speg.

*Anal. Mus. Nac. Buenos Aires* 6: 118. 1899.

**Type species:** *V. argentina* Speg.

**Syn.:** *Volvaria* Kummer, *Führ. Pilzk.*, p. 23. 1871. *Volvaria* (Fr.) Quél., *Champ. Jura Vosg.*, p. 114. 1873, non D.C. (1805).  
*Pseudofarinaceus* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 449. 1909, non ex O. Kuntze (1891).  
*Volvariopsis* Murr., *Mycologia* 3: 280. 1911.

**Characters:** Habit of the carpophores pluteoid; pigment present or absent; lamellae free; hymenophoral trama inverse; spore print sordid pink to brownish pink; spores smooth, inamyloid, stramineous under the microscope, with moderately thick wall, uni- or binucleate or mixed uni-bi-nucleate; basidia normal; cystidia often present; stipe central, always with a distinct membranous volva at the base; hyphae without clamp connections, in fewer species (e.g. *V. macrospora*) clamped. On the soil in and outside the woods, also on wood, on decaying agarics, on dung, on straw and other vegetable matter.

**Development of the carpophores:** Bulbangiocarpous and pileocarpous. A striking feature is the development of the pileus in a schizogenous cavity (Reijnders).

**Area:** Cosmopolitan, or nearly so.

**Limits:** The presence of a well developed volva seems to be a good characters, at

least in this family. Spegazzini intended to separate the species with "continuous" stipe in an autonomous genus, *Volvariella*. The type specimen of the type species is a true *Volvaria* in the sense of most modern authors. This means that Spegazzini's genus, if emended, can replace *Volvaria* which is a homonym.

**State of knowledge:** Many species have been described, yet the only monograph has been published for North American species. The enumeration of species known to this author is confined to 22 binomials. Like Shaffer (1951), we do not yet see fit to accept any sections within *Volvariella* inasmuch as there is no correlation between spore size and viscosity.

**Practical importance:** The genus *Volvariella* has as much economic importance as *Agaricus*. What the *Agaricus bisporus* culture is in the temperate climates, that is in the tropics the culture of *Volvariella\** *volvacea* and *V. diplasia*. These two species are grown in very large quantities in China, Indonesia, Malaya, India, Burma, Indo-China, on the Philippine Islands and Madagascar. The methods of this culture vary according to the availability of the substratum (usually waste products of some branch of tropical agriculture - very frequently rice straw). The fruiting bodies are sold in fresh condition in the markets and are exported in cans. In Czechoslovakia, *V. volvacea* appeared as "weed fungus" in mushroom (*Agaricus bisporus*) beds.

## SPECIES

### 1. Large-spored species (spores >12 µm long):

#### Stirps Speciosa.

*V. alabamensis* (Murr.) Shaffer (Volvariopsis, Murr.); *V. speciosa* (Fr. ex Fr.) Sing. (Volvaria, Kummer), var. *speciosa* and var. *gloiocephala* (D.C. ex Fr.) Sing.; *V. californica* (Earle) Sing. (Locellina, Earle); *V. earlei* (Murr.) Shaffer (Volvariopsis, Murr.); *V. stercoraria* (Peck) Sing. (Pluteus, Peck); *V. macrospora* Sing. ined.

### 2. Small-spored species:

#### Stirps Bombycina. (Pileus with non-appressed conspicuous fibrils.)

*V. bombycina* (Schaeff. ex Fr.) Sing. (Volvaria, Kummer); var. *bombycina* and var. *flaviceps* (Murr.) Shaffer.

#### Stirps Volvacea. (Medium to large species.)

*V. bakeri* (Murr.) Shaffer (Volvariopsis, Murr.); *V. volvacea* (Bull. ex Fr.) Sing. [Vaginata virgata (Pers. ex S.F. Gray); *V. esculenta* (Mass.) Sing. (Volvaria, Mass.) unless too close to the preceding species; *V. diplasia* (Berk. & Br.) Sing. (Volvaria, Sacc.).

#### Stirps Taylori. (Small pigmented species.)

\*See Singer, R. *Mushrooms and Truffles*. Leonard Hill, London NW 1. 1961, and S.T. Chang & T.H. Quimio, *Tropical Mushrooms*. Hong Kong. 1982.

*V. taylori* (Berk.) Sing. (*Volvaria*, Gillet); *V. fibrillosa* (Bres. in Rick) Sing. (*Volvaria* Bres. in Rick); *V. pseudovolvacea* (Berk. & Br.) Sing. (*Volvaria*, Sacc.); *V. murinella* (Quél.) Moser in Gams (*Volvaria*, Quél.); *V. villosovolva* (Lloyd) Sing. (*Volvaria*, Lloyd); *V. alachuana* (Murr.) Shaffer (*Volvariopsis*, Murr.), and a European species very close to it; *V. plumulosa* (Lasch) Sing. sensu Lange (non Quél.) [*V. parvula* (Weinm.) Orton sensu Kühner & Romagnesi non Weinm.].

Stirps *Pusilla*. (Small white species).

*V. pusilla* (Pers. ex Fr.) Sing. [*Volvaria*, Quél.; *Volvaria parvula* (Weinm.) Kummer; *Agricus*, Weinm. at nom nov. pro *A. pusillo* Pers. ex Fr. non Fr. ex Fr., but unnecessary]; *V. pubescens* (Peck) Sing. (*Volvaria*, Sacc.); *V. plumulosa* Lasch ex Quél.); *V. surrecta* (Knapp) Sing. [*Volvaria*, Ramsbottom; *Volvaria loveyana* (Berk.) Gillet]; *V. cycnopotami(a)* (Berk.) Sing. (*Locellina*, Sacc.); *V. argentina* Speg.

Additional species, apparently autonomous, but unknown to this writer, or insufficiently described:

*V. canalipes* (Murr.) Shaffer; *V. peckii* (Atk. in Peck) Shaffer; *V. cubensis* (Murr.) Shaffer; *V. smithii* Shaffer, all North American, and *V. arenaria* (Pat.) Sing. (*Pluteus*, Pat.), from Africa. Perhaps also *V. jamaicensis* (Murr.) Shaffer but probably identical with *V. pseudovolvacea*.

## 118. CHAMAEOTA (W.G. Smith) Earle

*Bull. N.Y. Bot. Gard.* 5: 446. 1909.

Type species: *Agaricus xanthogrammus* Ces.

Syn.: *Agaricus* subgenus *Chamaeota* W.G. Smith, *Clavis Agar.*, p. 15. 1870.

*Annularia* (Schulz.) Gillet, *Champ. Fr.*, p. 389. 1876, non Sternb. (1823), nec Hochst. (1841).

*Agaricus* subgen. *Annularia* Schulzer, *Verh. Zool.-Bot. Ges. Wien* 16: 49. 1866.

Characters: As in *Volvariella* but without a volva; annulus present; spore print between "Paloma" and "Sonora" M & P; spores between small and medium sized, ± ellipsoid; hyphae without clamp connections; epicutis not hymeniform. On wood, rarely on the earth in woods.

Development of the carpophores: Unknown.

Area: Probably cosmopolitan (except for the frigid zones), but with certainty only in Central and Eastern Europe, the Trans-Caucasian subtropical zone, and North America.

Limits: This genus differs from both *Volvariella* and *Pluteus* merely in the characters of the veil. It is impossible to tell at present whether, in this particular case, a distinction of a genus from two others on the basis of velar characters will prove to be artificial as it has been proved to be in several other cases. On the other hand, the distinction of the genus *Chamaeota* by the presence of the annulus cannot be rejected a priori, and its delimitation is extremely simple and convenient on the basis

of the present diagnosis. There is little likelihood that *Chamaeota* will be given up lightly, unless strong reasons can be given to support its suppression.

Under present circumstances, we may say that all species of *Chamaeota* are at least partly yellow; the hyphae of the epicutis are cylindric-filamentous as in sect. *Hispidoderma* Fay. of *Pluteus*. The group of species thus circumscribed, is very homogeneous and natural. On the other hand, species with pseudoamyloid spores, with germ pore, or with a distinct metachromatism in cresyl blue cannot be considered as belonging in *Chamaeota*; they all have regular rather than inverse trama, and are here referred to the *Agricaceae*.

*State of knowledge:* The type species is incompletely known. No specimens have been available to any modern author, and the description given by Cesati has not been emended. However, the diagnosis as published originally by Cesati is fully correct for a species of *Chamaeota*, and his guess at *Pluteus* is very significant. It is conceivable that Cesati confused some species of the family Agaricaceae but the thin stipe does not favor this interpretation. Consequently, no immediate danger to the generic name *Chamaeota* can be seen. If type specimens of the type species are in existence they are perhaps conserved in Naples; there are no specimens at Kew. Three species are well known.

*Practical importance:* None.

## SPECIES

Aside from the type species (see above): *C. sphaerospora* (Peck) Kauffm. (*Annularia*, Peck); *C. mammillata* (Longyear) Murr. (*Annularia*, Longyear), possibly conspecific with *C. sphaerospora*; *C. fenzlii* (Schulzer) Sing. (*Annularia*, Gillet).

### 119. PLUTEUS Fr.

*Genera Hymen.* p. 6. 1836.

*Type species:* *Agaricus pluteus* Batsch ex Fr., synonymis exclusis (= *Pluteus cervinus* = *P. atricapillus*).

*Syn.:* *Rhodosporus* Schröter in Cohn, *Krypt.-Fl. Schlesien*, p. 617. 1885-9.

*Characters:* Habit of the carpophores pluteoid (Pl. 69, 1, ca); pileus with hymeniform, or cellular epicutis, or the hyphae of the epicutis filamentous, allantoid, or cylindric fusoid and not hymeniform; lamellae free, spores usually ovoid or (short-) ellipsoid, more rarely subcylindric or globose, with moderately thin, smooth, non-amyloid, stramineous, homogeneous wall, usually rather small to medium, rarely rather large, usually uni-nucleate; basidia normal; cystidia often metuloids or lepto-cystidia, more rarely pseudo-paraphysis-like, sometimes with characteristic hooks (Pl. 21, 2; 69, 2 me, C), in few species only cheilocystidia present; hymenophoral trama inverse; stipe central, usually fleshy-subfibrillose; veil strongly reduced, ap-

pendiculate-cortinoid, or volvate-cortinoid, indistinct, fugacious (Pl. 64, 2), or much more frequently absent; context of the pileus most frequently white, consisting of fleshy, inamyloid tissue; hyphae with or without clamp connections; on various substrata, on dead and living plant tissue, on humus and sand, but most frequently on decayed wood in the forests (Pl. 21, 2; 69-71).

*Development of the carpophores:* Gymnocalypous (*P. atricapillus*), pilangiocarpous (*P. chrysphlebius*), or paravelangiocarpous (*P. granulatus*, *P. latifolius*); - pileostipitocarpous in most species.

*Area:* Definitely cosmopolitan, excepting Antarctica.

*Limits:* *Pluteus* is not close to any other genus except for *Chamaeota* and *Volvariella*.

*State of knowledge:* This genus is comparatively well studied in Europe, North and South America, less well in Asia and Africa. The following enumeration admits 150 species known to the present author.

*Practical importance:* In spite of the excellent culinary qualities of some of the *Plutei*, representatives of this genus are rarely found in the markets and are also rarely used by amateurs. The wood-destroying properties of some species are limited to previously decayed, dead wood or at least dead tissue on living trees; this, however, is valid only for the most common species, and exceptions will probably be found. *Pluteus* contains no mycorrhizal species. The bluing species incl. *P. salicinus* are probably hallucinogenic.

## SPECIES

Sect. 1. *PLUTEUS* (*Trichoderma* Fayod 1889, *Tricholomatae* Lange, 1917, *Fibrillosi* Imai 1938). Epicutis of pileus with elongated, pilose or hyphous elements which are mostly apposite or suberect in fascicles, especially in the center of the pileus, gelatinized or more often not gelatinized; spherocysts, none. Hyphae either with or without clamp connections. Metuloids (Pl. 69, 1 me) numerous, with partly or entirely thickened wall and deep-rooting pedicel, with an apex characterized by the presence of prongs, hooks, spinules and other excrescences, sometimes with acute tooth-like excrescences even on the sides of the metuloids, fewer metuloids, especially near the edges of the same lamellae without excrescences (Pl. 69, 1 meM), and one species with consistently entire metuloids, and then reminding one of the metuloids of *Inocybe*.

*Type species:* *Agaricus pluteus* Batsch ex Fr.

*Stirps Pellitus.* (Clamp connections present. Pigment none.)

*P. pellitus* (Pers. ex Fr.) Kummer.

*Stirps Subcervinus.* (Clamp connections present; all cheilocystidia hyaline; pigment gray to fuscous to black.)

*P. brunneidiscus* Murr.; *P. subcervinus* (Berk. & Br.) Sacc.; *P. washingtoniensis*

Murr. (probably conspecific with *P. brunneidiscus*); *P. fibulatus* Sing. in Sing. & Digilio; *P. nigropallescens* Sing.; *P. mesosporus* Sing.; *P. shii* Hongo.

Stirps *Glaucus*. (As preceding stirps, but pigment of epicutis glaucous.)

*P. glaucus* Sing.

Stirps *Salicinus*. (Clamp connections, cheilocystidia and pigment of pileus as in stirps *Subcervinus*, but base of stipe with blue or green pigment at least internally, and reacting positively with phenol, rarely without discolored stipe base and then recognizable by gray pileus with dark erect scales in center, and gray base of stipe.)

*P. salicinus* (Pers. ex Fr.) Kummer, with var. *salicinus* and var. *achloes* Sing.

Stirps *Atromarginatus*. (Clamp connections generally present; many or all cheilocystidia filled with a pale fuscous to dark sepia sap, therefore edge of lamellae more or less discolored. Rare occasional forms clampless.)

*P. spegazzinianus* Sing.; *P. atromarginatus* (Konrad) Kühner [*P. cervinus* var. *nigrofloccosus* R. Schulz 1930; *P. cervinus* var. *atromarginatus* Sing. 1925; *P. cervinus* ssp. *atromarginatus* Konrad 1927; *P. nigrofloccosus* (R. Schulz) Pilát]; *P. aporus* Sing. with f. *porpophorus* Sing. and f. *aporus*; *P. eucryphiae* Sing.; *P. martinicensis* Fiard & Sing. ex Pegler.

Stirps *Spinulosus*. (Clamp connections present. Metuloids in contrast to stirps *Subcervinus* with which it otherwise coincides, showing abundant lateral spinules, fewer acute and entire.).

*P. spinulosus* Murr.

Stirps *Horridus*. (Clamp connections present; metuloids away from the edge of the lamellae without horns or appendages.)

*P. horridus* Sing.

Stirps *Viscidulus*. (Clamp connections absent. Pigment absent.)

*P. viscidulus* Sing. in Sing. & Digilio.

Stirps *Harrisii*. (Clamp connections absent. Pigment present. Prongs of metuloids present but characteristically low and obtuse, or prongs horizontal and recurved but not attenuated from a broad base to a simple or crested apex. Generally tropical species.)

*P. harrisii* Murr. (*P. cervinus* var. *bambusinus* Baker & Dales); *P. angustisporus* Sing.

Stirps *Cervinus*. (Like preceding stirps but metuloids of the *Cervinus*-type exclusively present, or both metuloids of the *Magnus*-type and *Cervinus*-type present, i.e. at least some fusoid, with decidedly thick walls and strong prongs present.)

*P. atricapillus* (Secr.) Sing. (Agaricus, Secr.; *A. pluteus* Batsch ex Fr.; *P. cervinus* (Schaeff. ex Fr. 1838) Kummer); *P. minor* (Sing.) Sing.; *P. curtisii* (Berk. & Br.) Sacc.; *P. agloeothelos* (Berk. & Br.) Sacc. (*P. patricius* Schulz in Kalchbr.)

Boudier); *P. leianus* (Berk. ex Sacc.) Sing. (*Pluteolus*, Sacc.); *P. lilacinus* (Mont.) Sing.; *P. xylophilus* (Speg.) Sing.; *P. stephanobasis* Sing.

Stirps *Magnus*. (Like the preceding stirps but metuloids of the *Magnus*-type, i.e. tapering gradually from below the middle with small hooks, often acute, sometimes moderately thick-walled and often with some lateral spines; metuloids of the *Cervinus*-type absent; cheilocystidia all elongated cylindric-subclavate, more rarely dimorphic, i.e. short, vesiculose cheilocystidia also present.

*P. magnus* McClatchie; *P. petasatus* (Fr.) Gillet.

Stirps *Amphicystis*. (Clamp connections absent; pigment present, yellow to melaleucus in the pileus; metuloids without prongs, reminding one of those of *Inocybe*).

*P. amphicystis* Sing.; apparently also *P. reticulatus* Murr. according to the type analysis by Smith & Stuntz and redescription from African material by Pegler (1968).

Sect. 2. *HISPIDODERMA* Fayod (1889) (*Trichodermei* Lange 1917). Like the preceding section but cystidia not metuloid (sometimes with an outer resinaceous shell but wall proper thin-walled); clamp connections absent, only in few species present.

Type species: *P. leoninus* (Schaeff. ex Fr.) Kummer.\*

Stirps *Nigrolineatus*. (Clamp connections numerous.)

*P. umbrinidiscus* Murr.; *P. avellaneus* Murr. em. Sing.; *P. nigrolineatus* Murr.; obviously also *P. brunneisucus* Pegler.

Stirps *Umbrosus*. (Clamp connections absent or very exceptional; cystidia or cheilocystidia or both filled with dissolved intracellular (basically vacuolar) brown or fuliginous pigment; pileus and stipe both neither red nor yellow; spores ellipsoid to subglobose.)

*P. fernandezianus* Sing.; *P. jaffuelii* (Speg.) Sing.; *P. umbrosus* (Pers. ex Fr.) Kummer (*P. granularis* Peck); *P. multistriatus* Murr.; *P. fibrillosus* Murr. em. Sing., non Rick; *P. subfibrillosus* Sing. (*P. hiatulus* Romagn.); *P. compressipes* Murr.; *P. espeletiae* Sing.

Stirps *Aethalus*. (Like the preceding stirps, but spores subglobose or almost so, up to 6.5 µm. Small tropical species.

*P. aethalus* (Berk. & Curt.) Sacc.; *P. tephrostictus* (Berk. & Curt.) Sacc.; apparently also *P. lepiotiformis* Murr. (according to type study by Smith & Stuntz).

Stirps *Circumscissus*. (Like the two preceding stirpes but with marginate bulb.)

*P. circumscissus* Sing.

\*In his copy of Saccardo's *Sylloge 5*: 675. 1887 (at University of Lausanne), Fayod inserted a colored picture on the margin; it represents the species as understood by me - a yellow fungus belonging to this section.

Stirps Leoninus. (Pileus and/or stipe either red or yellow, orange bronze color etc.)

This stirps, Leoninus, is obviously not a fully natural unit, but very convenient for the moment.

*P. roseipes* Höhnel (*P. carneipes* Kühner); *P. glabrescens* Murr.; *P. sororius* (Karst.) Karst.; *P. luteomarginatus* Rolland (*P. romellii* (Britz.) Sacc.); *P. leoninus* (Schaeff. ex Fr.) Kummer; *P. longipes* Murr. (*P. whiteae* Murr.); *P. flavofuligineus* Murr.; *P. glyphidatus* (Berk. & Br.) Sacc.; *P. citrinus* Murr.; *P. conizatus* (Berk. & Br.) Sacc.; *P. rubrotomentosus* Sing.

Stirps Fuliginosus. (Characterized by the subacute or acuminate-subacute terminal cells of the epicutal trichodermium.)

*P. fuliginosus* Murr.; *P. rhoadsii* Murr. (unless too close to the preceding species); *P. argentinensis* Sing.; *P. yungensis* Sing.; *P. pluvialis* Sing.; *P. drepanophyllus* (Schulz. in Kalchr.) Singer (*Agaricus*, Schulz.); *A. villosus* Bull. sensu Decary, Kühn. & Romagnesi); apparently also *P. pallidecervinus* Murr.

Stirps Semibulbosus. (Young or old, or both young and old, pileus practically pigment-less.)

*P. semibulbosus* (Lasch ap. Fr.) Gill. sensu Kühn. & Romagn. [*P. gracilis* (Bres.) Lange ss. Lange; *P. boudieri* Orton]; *P. aquosus* Sing.; *P. haywardii* Sing.; *P. niveus* Murr.; *P. myceniformis* Murr.

Stirps Spilopus. (Pileus not venose, but fibrillose in center and with appressed long radial fibrils otherwise; spores not globose; cystidia hyaline inside; epicutis-cells not subacute. Colors not bright (neither yellowish nor reddish) but pileus always well pigmented. Cystidia not with a rigid complete incrustation. Mainly tropical species.)

*P. rimosellus* Sing. in Sing. & Digilio; *P. albostipitatus* (Dennis) Sing.; *P. fastigiatus* Sing. in Sing. & Digilio; *P. cubensis* (Murr.) Dennis (*Nolanea*, Murr.); *P. spilopus* (Berk. & Br.) Sacc.; *P. hispidulus* (Fr. ex Fr.) Gillet; *P. murinus* Bres.; *P. floridanus* Murr. ex Sing. (unless rather to stirps Nitens); *P. griseibrunneus* Murr.

Stirps Diptychocystis. [Differing from the preceding stirps mainly in the outer false (an incrustation!) walls of the cystidia. Temperate.]

*P. diptychocystis* Sing.

Stirps Atriavellaneus. (Clamp connections none. Pileus rarely reticulate-venose in center, often squamulose but not or very little radially fibrillose in the middle zone, more rarely granular almost all over, margin striate or sulcate, nor or not distinctly rimose, often more or less hygrophanous.

*P. sulcatus* Sing. in Sing. & Digilio; *P. plautus* (Weinm.) Gill.; *P. atrivellaneus* Murr., var. *atriavellaneus*, var. *parvus* Sing. and var. *flavidopubescens* Sing.; *P. hemalis* Sing.; *P. maculosipes* Sing.; *P. granulatus* Bres. (non ss. Kühner, Orton); *P. depauperatus* Romagn.; *P. kuthanii* Sing. ined.

Stirps *Cinerellus*. (As preceding stirps but elements of epicutis not erect-subhymeniform; pleurocystidia present; cheilocystidia not appendiculate; tropical and subtropical species.)

*P. cinerellus* Sing.; *P. rugososulcatus* Sing.

Stirps *Unakensis*. (Spores very small: mostly less than 4.2  $\mu\text{m}$  broad, and ellipsoid. Pileus fibrillose or silky.)

*P. unakensis* Murr.; *P. microsporus* (Dennis) Sing.

Stirps *Nitens*. (Like the preceding three stirpes but differing in globose spores, or at least with numerous globose spores in every print.)

*P. nitens* Pat.; *P. sergii* Sing.; *P. riberalensis* Sing. with var. *riberalensis*, var. *conquistensis* Sing., and var. *missionensis* Sing.

Stirps *Tomentosulus*. (Differing from stirpes Semibulbous, *Cinerellus*, etc. in tomentose stipe. Carpophores often rather large with thick-walled cystidiod elements in the covering of the stipe.)

*P. latifolius* Murr.; *P. tomentosulus* (Peck) Peck.

Sect. 3. *CELLULODERMA* Fayod (1889) (*Micaceae* Lange 1917; *Pruinosi* Imai 1938). Epicutis of pileus a hymeniform layer of relatively short (ellipsoid to saccate-obpiriform) elements, interrupted or not (sometimes representing the minority of the epicuticular elements!) by elongate cystidiod bodies which may be interpreted as dermatocystidia\*. Clamps none (but see Huijsman on *P. umbrinellus*, *Fungus* 25: 39, 1955.)

Type species: *P. nanus* (Pers. ex Fr.) Kummer.

Subsect. *Mixtini* Sing. (1956). Epicutis with dimorphic elements (Pl. 70, 1, 2e).

Type species: *P. psychriophorus* (Berk. & Br.) Sacc.

Stirps *Eugraptus*. (Edges of lamellae dark, cystidia brown, cheilocystidia brown; dermatocystidia obtuse.)

*P. eugraptus* (Berk. & Br.) Sacc.

Stirps *Longistriatus*. (Cystidia hyaline; margin of pileus strongly sulcate or pectinate. Dermatocystidia broadly rounded at their tip.)

*P. longistriatus* (Peck) Sacc.; *P. neophlebophorus* Sing.; *P. sanctixerii* Sing.; *P. variipes* Sing. with var. *atrociliollosus* Sing.; *P. oligocystis* Sing.

\*Smith & Stuntz (*Lloydia* 21: 131. 1958) have objected against the term dermatocystidia in this case, obviously not on the grounds of detailed morphological investigations but simply as a matter of opinion. Yet, since we are dealing with cystidiform elements in a hymeniform layer, the word is at least temporarily appropriate unless future studies should show them to be non-homologous with hymenial cystidia.

**Stirps Burserae.** (Differing from the preceding stirps in dermatocystidia which are narrowed to the obtuse or subacute, not broadly rounded tip.)

*P. burserae* Sing.

**Stirps Venosus.** (Pileus with short or indistinctly sulcate margin and rounded-obtuse dermatocystidia. Center of pileus rugose to venose.)

*P. subminutus* Sing.; *P. venosus* (Sing. ex) Sing.; *P. agriensis* Sing.

**Stirps Minutissimus.** (Dermatocystidia of pileus obtuse, attenuate towards tip, or broadly rounded. Center of pileus not rugose-venose. Margin not conspicuously sulcate or pectinate.)

*P. minutissimus* Maire; *M. seticeps* (Atk.) Sing.; *P. nanellus* Murr. (unless too close to *P. seticeps*); *P. umbrinoalbidus* Sing.; *P. substigmaticus* Sing.; *P. psychriophorus* (Berk. & Br. & Sacc.); *P. stigmatophorus* (Berk. & Br.) Sacc.

**Stirps Rimulosus.** (Epicutis of pileus less distinctly dimorphic, consisting of numerous elements intermediate between globose cells and dermatocystidia, and only very few spherocysts and strongly elongated elements.)

*P. polycystis* Sing.; obviously also *P. rimulosus* Kühn. & Romagnesi.

**Stirps Thomsonii.** (Like the preceding stirps but without cystidia. Cheilocystidia generally beaked.)

*P. thomsonii* (Berk. & Br.) Dennis (*P. cinereus* Quél.).

**Stirps Laetus.** (Differing from the preceding stirpes in its bright orange to red color; cheilocystidia generally beaked.)

*P. laetus* Sing. var. *laetus* and var. *mixtus* Sing.

Subsect. *Eucellulodermini* Sing. Elements of epicutis of pileus not dimorphic. Dermatocystidia not present (Pl. 71).

*Type species:* *P. nanus* (Pers. ex Fr.) Kummer.

**Stirps Chrysophlebius.** (Pileus with bright red, orange or yellow pigment, the latter either pale cinnamon to orange cinnamon and completely dissolved in epicuticular cells or these cells appearing hyaline, or yellowish in KOH.)

*P. aurantiorugosus* (Trog.) Sacc. [*P. aurantiacus* Murr.; *P. calocephalus* Atk.; *P. coccineus* (Mass.) Lange]; *P. laetifrons* (Berk. & Curt.) Sacc. with var. *laetifrons* and var. *boliviensis* Sing.: *P. chrysophlebius* (Berk. & Rav.) Sacc. with ssp. *chrysophlebius*, ssp. *sublaevigatus* Sing., and ssp. *bruchii* (Speg.) Sing. [conspecific: *P. admirabilis* (Peck) Peck; *Nolanea bruchii* Speg.]; *P. melleus* Murr. (according to type studies by Smith & Stuntz, unless too close to the preceding species).

**Stirps Globiger.** (Pileus, lamellae, stipe, and/or context with yellowish colors, pigment in most epicuticular cells pale fuscous to brown; pileus mostly not pure yellow, orange, red but at least with brown, fuscous, or melleous parts. Spores globose.

*P. globiger* Sing.; *P. xanthopus* Sing.; perhaps *P. fulvibadius* Murr.

Stirps Lutescens. (As preceding stirps but spores ellipsoid to subglobose.)

*P. chrysophaeus* (Schaeff. ex Fr.) Quél. (*P. xanthophaeus* Orton); *P. melleipes* Murr.; *P. lutescens* (Fr.) Bres.; probably some other European species unknown to me.

Stirps Luctuosus. (Pileus, stipe, lamellae and flesh without yellow, orange, red or melleous tones. Cystidia or cheilocystidia or both with fuscidulous sap, or contents.)

*P. luctuosus* Boudier; *P. beniensis* Sing.; *P. riograndensis* Sing. var. *riograndensis* and var. *atromarginatus* Sing.; *P. rimosoaffinis* Sing.; *P. fusconigricans* (Bk. & Br.) Sacc.

Stirps Roseocandidus. (Almost pigmentless species.)

*P. alborugosus* Kühn.; *P. hololeucus* Sing.; *P. roseocandidus* Atk.

Stirps Pulverulentus. (Pigment present and abundant, but not yellow, orange, red or melleous. Center of pileus typically rugose to venose reticulate. Spores, at least many in a print, globose.)

*P. pulverulentus* Murr., var. *pulverulentus*, and var. *pseudonanus* Sing.; *P. eliae* Sing.; *P. sapiicola* Sing.

Stirps Jamaicensis. (Differing from the preceding stirps only in subglobose to ellipsoid spores.)

*P. fluminensis* Sing.; *P. jamaicensis* Murr.; *P. nanus* (Pers. ex Fr.) Kummer sensu Sing. (1929), Orton (1960 as described *Nov. Hedw. Beih.* 29: 158. 1969); *P. fuligineovenosus* Horak; *P. paraensis* Sing. with var. *mexicanus* Sing.; *P. phlebophorus* (Ditmar ex Fr.) Kummer; *P. griseopus* Orton; *P. cinereofuscus* Lange; *P. pallescens* Orton; *P. dominicanus* Sing.; *P. rimosus* Murr.; obviously also *P. californicus* McClatchie.

Stirps Tucumanus. (Center of pileus consistently smooth, otherwise like preceding stirps.)

*P. tucumanus* Sing.; *P. fallax* Sing.; *P. iguazuensis* Sing.; *P. keissleri* Sing.; *P. ludovicianus* Murr.; *P. albolineatus* (Berk. & Br.) Sacc.; *P. ricardii* Sing.

## AGARICACEAE Fr.

*Syst. Orb. Veg.*, p. 65. 1825 (ut "subordo" Agaricini)\*; *Chev.*, *Flore Paris* 1: 121 1826 (ut "ordre" Agariceae); Cohn, *Hedwigia* 11: 17. 1872 (ut fam. Agaricaceae); em.

\*Neither the designation as subordo, nor the spelling of the ending invalidates the status of Fries's family in the author's opinion. Since there was no such status as families in the scheme used by Fries in *Systema Mycologicum*, or in *Systema Orbis Vegetabilis*, it is obvious that the taxon above the genus is meant to take the place of the modern family conception. Since this group was proposed long before it became customary to form family names in the fungi with the suffix aceae, and even longer before the International Rules recommended or decreed to do so, it is not unexpected to find Fries' name formed in

Type genus: *Agaricus* L. ex Fr.

Syn.: *Hymenini* Fr. Syst. Myc. 1: liv, lvi, 1821, p.p.

*Agariciformes* Schwein., Schr. Naturf. Ges. Leipzig 1: 78. 1822.

*Lepiotaceae* Roze, Bull. Soc. Bot. Fr. 23: 51. 1876 (nom. nud.), l.c., p. 111 (ut Lépiotées); Van Overeem, Bull. Jard. Bot. Buitenzorg 9: 19. 1927.

*Psalliotées* Roze, l.c., p. 51 (nom. nud.); p. 113.

*Polyphyllei* Quél., Enchiridion, p. 2. 1886 (lectotype: *Agaricus* L. ex Fr.), p.p.

*Leucocoprinaceae* Sing., Ann. Mycol. 34: 323. 1936 (nom. subnud.); Jülich, High Taxa Bas. p. 376. 1981.

**Characters:** Habit of the carpophores tricholomatoid or collybioid, or most frequently pluteoid, but usually showing a very characteristic appearance of its own because of the furfuraceous to scaly surface (often with a smooth disc, "calotte") and the annular veil; pileus often umbonate; epicutis consisting most frequently of a palisade (trichodermial palisade), but also often hymeniform, or forming an epithelium, or consisting of parallel, repent hyphae (cutis), or else consisting of repent, interwoven hyphae which surround single spherocysts (heteromorous); hymenophore lamellate\*; lamellae thin, free, or more rarely adnexed, adnate or decurrent; hymenophoral trama regular to irregular but never truly intermixed, and never bilateral, and also never inverse; basidia normal, i.e. without siderophilous granulosity and comparatively rather small, mostly 4-spored; cystidia present or absent; spore print most variable, pure white, cream color, ochraceous, green to olive, pink, purple, or sepia, sometimes changing color by dehydration (especially from green to purple); spores under the microscope hyaline to stramineous, or brownish, bay, or melleous, cyanophilic, exceptionally acyanophilic (in one species of *Cystoderma* and where very strongly pigmented) smooth or echinate, warty, punctate, echinulate-rough, etc., with comparatively thick simple wall or with complex wall and then rather thick-walled to very thick-walled, with or without germ pore, with or without a metachromatic (in cresyl blue) endosporium, with or without a persistent perispore, amyloid or inamyloid, or most frequently from slightly to very strongly pseudoamyloid, usually binucleate, very rarely uninucleate (according to Kühner); stipe central, often remote from the hymenophore by a collarium, often with a more fibrous structure than the soft-fleshy pileus, and then easily separable from the latter, with a membranous or cortinoid (usually membranous and funnel-shaped) veil which is in most cases at least temporarily, annuliform, and in some genera becomes movable very early; volva also present, or rudimentary, or completely absent; context fleshy, consisting of pseudoamyloid or much more frequently inamyloid hyphae with or without clamp connections. Pileus and context often strongly reacting (deep and rapid color reactions) with the usual reagents. Most frequently on the earth or on sand or humus in woods, but also on various dead or living plant tissues (Pteridophyta, wood of conifers and Angiospermae), also in

a different way. If we would not interpret the rules somewhat liberally in this particular case, i.e. when admitting family names that were not originally designated as families, or had not the accepted ending, we would undoubtedly find ourselves in nomenclatorial difficulties even more annoying than those we have to face at present.

\*Rick (in litt.) indicates a rare poroid (gastroid?) aberration of the hymenophore of an *Agaricus* sp. in Brazil [= *Boletus albidus* (Romagnoli) Mre.] but this may have been *Endoptychum*.

deep moss; very frequently in greenhouses, steppes and deserts, often in fields and sand dunes. Not ectomycorrhizal.

**Limits:** The Agaricaceae are somewhat intermediate between the group of families treated up to this point on one hand, and the dark-spored agarics (Coprinaceae, Bolbitiaceae, Strophariaceae) on the other hand. This is the reason why the Agaricinae as a suborder are considered continuous from the Polyporaceae to the Entolomataceae.

The delimitation of the family will be discussed in the chapter on "Limits" in the respective genera (*Agaricus*, *Cystoagaricus*, *Crucispora*, *Chamaemyces*, *Squamanita*, *Cystoderma*, *Phaeolepiota*, *Ripartitella*, *Macrometula*, *Psathyrella*, *Pholiota*, *Simocybe*).

#### KEY TO THE TRIBUS

- A. Spores pseudoamyloid; endosporium metachromatic in cresyl blue mounts and/or germ pore very broad and conspicuous; spore print never brownish-purple; lamellae free, often remote from the stipe by a "collarium" (a smooth zone). *Leucocoprineae*, p. 467
- A. Spores either not pseudoamyloid, or, if pseudoamyloid, devoid of any (red) metachromatic zone inside the episporium in cresyl blue mounts and generally devoid of any kind of germ pore; spore print white or brownish purple to sepia, sometimes yellow-cream, pinkish purple or olive green to blue green; lamellae free or variously attached.
  - B. Spore print brown, brownish purple or sepia, or olive green to blue-green, often becoming pinkish purple after dehydration (if green, becoming purple, the spore wall is heterogeneous, otherwise homogeneous). *Agariceae*, p. 482
  - B. Spore print white, cream, palest orangy pink or light violet or yellow.
    - C. Pigments sparse or none; epicutis - a cutis of repent, hyphae forming a silky surface; spores metachromatic in cresyl blue mounts; veil present (see *Leucocoprineae*).
      - C. Not combining these characteristics.
        - D. Lamellae free; hyphal elements of stipe mostly cenocytic. *Lepiotear*, p. 443
        - D. Lamellae not free or at least frequently adnate to adnexed; hyphal cells of the stipe mostly binucleate. *Cystodermateae*, p. 502

#### Tribus *Leucocoprineae* Sing.

*Pap. Mich. Ac. Sc., Arts & Lett.* 32: 141. 1946 (publ. 1948).

**Type genus:** *Leucocoprinus* Pat.

**Characters:** Those of the family; spores with complex wall, smooth or ornamented (sometimes ornamentation only in an immature state), not with ornamentation type XI and heterogenous wall, endosporium  $\pm$  distinctly metachromatic in cresyl blue mounts, with a broad germ pore or with an indistinct very narrow germ pore, more rarely without a distinct germ pore; pseudoamyloid; hyaline or subhyaline; annulus often movable; volva often well developed; lamellae free.

## KEY TO THE GENERA

- A. Spore print green or olive when fresh, rarely ochraceous; context often reddening when bruised; often containing a poisonous substance.
- B. Volva very distinct; spores small. 120. *Clarkeinda*, p. 468
- B. Volva none, or extremely fugacious; spores medium to large. 121. *Chlorophyllum*, p. 470
- A. Spore print white, cream, pink.
- C. Clamp connections present (but sometimes scanty - look for them in the rind layer of the stipe).
- D. Volva well developed, cup-shaped; spore print white. 122. *Volvolepiota*, p. 471
- D. Volva none, or extremely fugacious; spore print white, cream or pink.
- E. Margin of pileus not long-pectinate nor yellow; most species rather characteristically very large and with scaly pileus-surface; spore wall taking up Congo red in alkalic solution (becoming freely pink); metachromatic endosporium rather broad (if a fresh spore print is not available and context reddens, always compare "B" above). 123. *Macrolepiota*, p. 472
- E. Margin of pileus long-pectinate, or pileus yellow, or spore wall taking up Congo red in alkalic solution only very weakly and partially; metachromatic endosporium often very narrow (see "G" below).
- C. Clamp connections absent in the trama of pileus and stipe.
- F. Pileus with darker scales on pallid ground; carpophores large, habit of *Macrolepiota*; spores larger than 9  $\mu\text{m}$  or reaching up to 20  $\mu\text{m}$ , with broad, truncate germ pore, with the medulla not purple red in cresyl blue; the epicutis not a cutis, but palisadic, never mainly composed of spherocysts (see "E" above).
- F. Pileus and habit different; spores in 4-spored carpophores rarely larger than 12.5  $\mu\text{m}$ , with or without a distinct germ pore but pore often rudimentary (reduced to a narrow tract) or purple red in cresyl blue mounts.
- G. Pileus and stipe typically without darker scales of any kind and typically pigmentless (basically white), thin, fragile; pileus silky or radially fibrillose in age, with a cutis consisting of smooth, elongated hyphae; spores without a germ pore or with a rudimentary one; smooth; spore print white; context not discoloring when bruised (not reddening). 126. *Sericeomyces*, p. 481
- G. Not combining the characteristics indicated above.
- H. Margin of pileus not or eventually very short pectinate; basidia monomorphic; conspicuous pseudoparaphyses uncommon or absent, more rarely present. 124. *Leucoagaricus*, p. 474
- H. Margin of pileus early long-pectinate, hymenium mostly of the *Psathyrella*-subtype of Buller. 125. *Leucocoprinus*, p. 479

### 120. CLARKEINDA O. Kuntze

*Rev. Gen. Pl.* 2: 848. 1891.

*Type species:* *C. poderes* (Berk. & Br.) O. Kuntze.

*Syn.:* *Chitonia* (Fr.) Karst., *Bidr. Finl. Nat. Folk.* 32: 274. 1879, non aut. prior.

*Agaricus* subgen. *Chitonia* Fr., *Hymen. Eur.*, p. 287. 1874.

*Chitonella* Mass., *Brit. Fung. Fl.* 1: 418. 1892 (hyponymous).\*

*Chitonella* Henn. in Engler & Prantl, *Nat. Pfl.-Fam.* I. 1\*\*: 240. 1898.

*Chitonis* Clements, *Gen. Fungi*, p. 114. 1909.

\*It is difficult to decide whether Massee's genus should be considered as validly published. He says: "... to be consistent, the genus *Chitonia* Fries, including both ringed and ringless species, must be divided into two genera, *Chitonia* including the species without ring, and the species furnished with a ring included in a genus that might be called *Chitonella*." The only species indicated by Massee for *Chitonia* is *C. rubriceps*, now considered as the type species of the genus *Macrometula*. The true Chitonias (= *Clarkeinda*) are either annulate or exannulate. If Massee actually proposed a new genus (the words "might be called" do not suggest it) in the text quoted above, it is still doubtful whether he considered as

**Characters:** Pileus usually scaly, fleshy; spore print green to olive when fresh (darkening by dehydration to 15 L 8 M&P in spore preparations); spores rather small (much less than 10  $\mu\text{m}$  long), ellipsoid to ovoid with distinct thin or broad, truncate germ pore, with compound but relatively thin, avelleanous (KOH) wall, smooth, pseudoamyloid, very weakly metachromatic in cresyl blue; cystidia none on the sides of the lamellae; cheilocystidia subvesiculose; hymenophoral trama rather regular at first, becoming irregular, hyphae without clamp connections and annulus usually complex, movable; volva basal, cup-shaped, firm, persistent and never anuliform. On the ground.

**Development of the carpophores:** Obviously "hemiangiocarpous" but not studied in detail.

**Area:** Tropical Asia.

**Limits:** This genus is evidently closest to *Chlorophyllum*, and some authors will prefer to consider these genera as synonyms whereby *Clarkeinda* would emerge as the valid name. However, there are several important characters separating *Chlorophyllum* and *Clarkeinda*, among them the smaller spores, and the volva of *Clarkeinda*. Boedijn, in fact, thinks that *Clarkeinda* is closer to *Agaricus* whereas *Chlorophyllum* is closer to *Lepiota* (what he has in mind, is *Macrolepiota*). The author has studied the type but the type specimens are all completely immature, but a recent collection by Lealavathy from the Calicut University campus, India (F) provided all the missing data. The color of the spore print is indicated as green or olive by Boedijn as well as by Petch, the only authors who have published on this fungus from detailed personal knowledge of the fresh fungus. The indications of purple brown spores may be based on a discoloration phenomenon comparable to what is known in *Melanophyllum* or else it may be based on imprints of the lamellae on white paper caused by the autoxidation (the flesh reddens when touched) of the cell sap. In the latter case the indication of purple brown spores must be considered as a plain misstatement.

Otherwise, this genus is well separated from all other agarics, in the tribus *Leucocoprinae* as well as in other groups.

**State of knowledge:** The work previously done on the only representative of this genus by Petch, Boedijn, and Singer makes it absolutely certain that *Clarkeinda* belongs in the Agaricaceae, and is closest to *Chlorophyllum*.

**Practical importance:** Unknown.

## SPECIES

*C. trachodes* (Berk.) Sing. (*Agaricus*, Berk.; *Chitoniella*, Petch; *Agaricus poderes* Berk. & Br.; *Chitonnia*, Sacc.; *Clarkeinda*, O. Kuntze; *Chitoniella*, Henn.).

the type of the emended *Chitonnia* his *C. rubriceps*, or one of Fries' exannulated Chitonias. In the first case, his attitude would not be conform with the type method; therefore, the other alternative is assumed to be true. Consequently, *Chitonnia* and *Chitoniella* in Massee's sense are here considered to be congeneric and identical and synonymous with *Clarkeinda*.

## 121. CHLOROPHYLLUM Massee

Kew Bull. for 1898: 135. 1898.

Type species: *C. esculentum* Mass. [*C. molybdites* (Meyer ex Fr.) Mass.].

**Characters:** Those of the tribus; habit of the carpophores similar to that of the species of *Macrolepiota*; pileus scaly; epicutis consisting of a palisade of erect hyphae on the disc, the palisade soon broken and fasciculate-twisted on the margin, or disappearing from the margin inward; lamellae usually becoming green in age, quite free and remote from the stipe; spore print green (various shades, not constant\*), or more rarely "colonial buff" (Ridgway); spores smooth with thick, complex wall which is stained by Congo red in alkalic mounts only weakly or not at all and colorable with cresyl blue in all their parts (therefore indistinctly metachromatic in fresh or recently dried material), with broad germ pore, with an intermembranal space visible in phloxine mounts, large; cystidia none on the sides of the lamellae; cheilocystidia present; hymenophoral trama almost regular becoming irregular with age; stipe elongate (longer than the diameter of the stipe in most individual carpophores), with a bulb at the base, without a cup-shaped volva, with movable annulus which is somewhat fixed in youth but becomes free on drying, and is complex as in *Macrolepiota*; context inclined to redden when bruised, often containing a poisonous matter; hyphae inamyloid, with clamp connections but many septa without clamps. Mostly on rich soil, under trees, often in gardens and plantations.

**Development of the carpophores:** "Hemiangiocarpous". Not known in detail but hardly different from *Macrolepiota*.

**Area:** Tropical America, Oceania, Asia, Africa, north to North America (Florida to New York and Michigan), south to Buenos Aires.

**Limits:** See under *Macrolepiota*, *Leucoagaricus*, and *Clarkeinda*.

**State of knowledge:** A complete study of *C. molybdites* has been made by Singer (*Mich. Ac. Sc. Pap.* 32: 137. 1947). It will probably be possible to distinguish several races within *C. molybdites* according to the intensity of the reddening, the exact tone of the spore print, perhaps also the amount of poisonous matter in the fruiting bodies, and according to the relative frequency of clamp connections. It is unknown whether and which of these characters will correspond to a given area's population; therefore it is not known whether these variations are geographic races inasmuch as one has the impression that most of the localities known in the Americas have only adventitious populations.

**Practical importance:** *C. molybdites* is poisonous in North America, Southern South America, and the Philippines. It has been reported to be edible in South America in one instance, but this indication should be accepted with caution. It may well be that a certain kind of preparation "depoisons" the fungus, or that the

\*The spore print of the original material on which *Lepiota morgani* Peck was based, is now preserved at the Farlow Herbarium, and has faded to "powdered gold" (Maerz & Paul).

amount of poisonous matter is very variable. The poisonous matter has been studied pharmacologically (studies carried out at the University of Buenos Aires in 1965-66); these data coincide well with the data published by Floch, Lebarbe & Roffi, *Rev. Mycol.* 31: 317-322. 1966. If there are two different species - one edible, one poisonous, - a possibility I consider unlikely - the morphological and anatomical characters which separate them, are insufficiently elaborated. The edible one would be *C. esculentum* Mass., the poisonous one *C. molybdites*. The toxic substance has been studied by Eilers & Nelson (*Toxicon* 12: 557-563. 1974).

## SPECIES

*C. molybdites* (Meyer ex Fr.) Mass. [*Leucocoprinus*, Pat.; *Lepiota*, Sacc.; *Agaricus guadelupensis* Pat.; *Lepiota morgani* (Peck) Sacc.; *Annularia camporum* Speg.; *Agaricus glacioui* Berk.]; *C. esculentum* Mass. (cf. Singer, *Sydowia* 9: 401. 1944, unless too close to the preceding species).

### 122. VOLVOLEPIOTA Sing.

*Bol. Soc. Arg. Botan.* 8: 12. 1959.

*Type species: Lepiotella brunnea* Rick.

*Syn.: Lepiotella* Rick, *Lilloa* 2: 251. 1938, non (Gilbert) Gilbert ex Kühner & Maire (1934).  
*Rickella* Locquin, *Bull. Soc. Mycol. Fr.* 68: 1952, non *Rickiella* Sydow apud Rick (1904).

*Characters:* Same as in *Macrolepiota*, but differing in the presence of a well-formed cup-like volva. The spore print is white. Clamp connections present. Spores medium sized, strongly pseudoamyloid, metachromatic in cresyl blue mounts. Context reddening (Pl. 72, 1-4).

*Development of the carpophores:* Obviously "hemiangiocarpous", not known in detail.

*Area:* South Brazil and Northern Argentina.

*Limits:* This genus is obviously closely related to *Clarkeinda* and *Macrolepiota*, easily distinguishable from the former by the white spore print and from *Macrolepiota* in the presence of a well-formed volva.

*State of knowledge:* Two species are known.

*Practical importance:* Unknown.

## SPECIES

*V. brunnea* (Rick) Sing. (*Lepiotella*, Rick); *V. albida* Sing.

*Pap. Mich. Acad. Sc.* 32: 141. 1946 (publ. 1948).

*Type species:* *M. procera* (Scop. ex Fr.) Sing.

*Syn.:* *Leucocoprinus* subgenus *Eu-Leucocoprinus* Locquin, *Bull. Soc. Linn. Lyon.* 14: 30. 1945.

*Characters:* Those of the tribus; spore print pure white, or pale pink, spores distinctly and strongly metachromatic in cresyl blue, and not uniformly deep blue under any circumstances, with a broad germ pore, smooth, very voluminous (above 10 µm in length and sometimes reaching 25 µm); cystidia none on the sides of the lamellae; pileus scaly, more rarely merely granulose, but smooth on the disc ("calotte") which has a cuticle made up by a palisade of long, usually straight elements (sometimes, however, the palisade becomes appressed with repent bunches of more or less agglutinate hyphae); annulus movable, consisting of hyphae with clamp connections (at least in normal, i.e. heterothallic individuals), more rarely without clamp connections; volva initially present but indistinct, and not persistent. On the soil in and outside the woods.

*Development of the carpophores:* Bivelangiocarpous, pileocarpous (also isocarpous sec. Watling).

*Area:* Almost cosmopolitan.

*Limits:* Some authors still call all the Agaricaceae either *Lepiota* or *Agaricus*. In this delimitation, the genus *Lepiota* would be of enormous size, and would contain the most extreme elements. In this regard, the situation is much like that in the boletes before they were revised. Heim and Romagnesi recognize both this genus (under the name *Leucocoprinus*) and *Hiatula* (i.e. *Leucocoprinus*) in addition to *Lepiota*. These authors leave *Chlorophyllum* in *Macrolepiota* (or as they call the latter: *Leucocoprinus*) because of the similarity of the macroscopical characters as well as most microscopical characters. However, the spore print is different in the two genera, a character which in itself, unless accompanied by the other correlated characters, would be insufficient to separate *Chlorophyllum* on a generic basis. The author (1939) also agreed to this point of view. But, since then, the correlated characters have come to the attention of the taxonomists, viz. the scarcity of clamp connections, the poisonous properties, and the different behavior of the spores in a mount first stained with cresyl blue and then with phloxine whereby an intramenbranal space remains pink while a strong solution of cresyl blue alone dyes the spores so deeply blue that often no distinct metachromasy can be observed. Even sharper is the distinction of both genera by the capacity of the spore wall to absorb Congo red in alkalic mounts as pointed out by Weresub (*Can. Journ. Bot.* 49: 2059-60 with color plate) and corroborated by the present author. With regard to the poisonous species, the situation is reversed: The only poisonous species of *Macrolepiota* has no clamped septa in the trama at all. All these characters of *Chlorophyllum* distinguish it from *Macrolepiota*. One may also add the predominantly tropical and subtropical distribution of *Chlorophyllum* as compared with the cosmopolitan but predominantly temperate distribution of *Macrolepiota*. *Leucogarius* differs from *Macrolepiota* in the absence of clamps, in addition to a few minor characters as indicated in the key (p. 268).

*State of knowledge:* The most important species of the northern temperate zone are comparatively well known, especially the type species. Locquin has added a few species to those previously known but it is doubtful whether or not the reddening of the context is actually a constant character. The author has studied a very large collection of *Leucoagaricus bresadolae* from a greenhouse in Massachusetts; some of the carpophores - all equally fresh - stained strongly, others were absolutely unchanging on exposure, while still another group showed slight discoloration. As the usual chemical reactions which are ordinarily as characteristic for this species as is the reddening of the context, have proved to be entirely parallel to the reaction induced by the oxygen of the air, the author concluded that had these specimens been collected in small number and at different locations in the open country, they may have been split into at least two different species. Therefore, it appears that the description of new species exclusively on the basis of the characters of autoxidation in *Leucocoprineae* is at least subject to skepticism, and the author does not accept this character as a basic one for the subdivision of the genera of the *Leucocoprineae*. On the other hand, there are undoubtedly many more species in existence than the nine indicated below. Many described species which are preserved in various herbaria have not yet been restudied, and it is very probable that some of them will be transferred to *Macrolepiota* as soon as careful type studies show that they belong in this genus.

*Practical importance:* All species of sect. *Macrolepiota* tested thus far have been found to be edible. Some are first rate mushrooms that are highly priced in the European, Asiatic and African markets, especially *M. procera*. They have not yet been grown in mushroom houses. They all fruit with great regularity at the same places year after year in spite of the fact that they are not mycorrhizal. At least one species, *M. venenata*, is poisonous.

## SPECIES

Sect. 1. *MACROLEPIOTA*. Some clamp connections present in the trama of the carpophores, or at least in the lower part of the rind of the stipe and at the base of many basidia.

*Type species:* *M. procera* (Scop. ex Fr.) Sing.

*M. procera* (Scop. ex Fr.) Sing. (*Lepiota*, Kummer; *Leucocoprinus*, Pat.); *M. mastoidea* (Fr.) Sing. (*Lepiota*, Kummer; *Leucocoprinus*, Sing. 1939); *M. rachodes* (Vitt.) Sing. (*Lepiota*, Quél.; *Leucocoprinus*, Pat.); *M. kerandi* (Speg.) Sing. (*Lepiota*, Speg.); *M. bonaerensis* (Speg.) Sing. (*Agaricus*, Speg.); *M. olivascens* Moser in Moser & Sing.; *M. zeyheri* (Fr.) Sing. (*Agaricus*, Fr.); apparently also *Leucocoprinus minutulus* Sing.; *Lepiota albuminosa* (Berk.) Sacc., and *Macrolepiota dolichaula* (Berk. & Br.) Pegler & Rayner.

Sect. 2. *MACROSPORAE* (Sing.) Bon (1981). Clamp connections on the hyphae of the trama consistently absent, or present only at base of cheilocystidia (Bellù, *Boll. Gr. Mic. Bres.* 25: 109. 1982) and along the hymenopodium (Malençon, *Sydotia, Beih.* 8: 265. 1979).

*Type species: M. excoriata* (Schaeff. ex Fr.) Moser.

*M. excoriata* (Schaeff. ex Fr.) Moser; *M. venenata* Jac. ex Blum; apparently also *M. konradii* (Huijsman ex Orton) Moser and *M. fuligineosquarrosa* Malençon.

## 124. LEUCOAGARICUS (Locquin) Sing.

*Sydotia* 2: 35. 1968.

*Type species: Leucoagaricus macrorhizus* (Locquin) Sing.

*Syn.: Leucocoprinus* subgenus *Leucoagaricus* Locquin, *Bull. Soc. Linn. Lyon* 12: 92. 1943.  
?*Attamyces* Kreisel, *Zeitschr. f. Allg. Microbiol.* 12: 648. 1972.\*

*Characters:* Those of the tribus; spore print pure white, sordid cream color, cream-orange, or pale lilac-pink, flesh cream (more flesh-colored than Ib of Romagnesi, Russules), under the microscope spores usually below 10 µm in length, in few species larger, often with a germ pore but this not always truncate but frequently extremely narrow or in form of a stopper- or lens-like plug, or pore in some species entirely wanting, with bi-to pluristratous wall which is either smooth or ornamented, sometimes with nail-like or wart-like to reticulate exosporial excrescencies, always metachromatic in cresyl blue (but the metachromatic endosporium in some species extremely thin); hyphae without clamp connections, inamyloid; annulus fixed, finally becoming ± movable or remaining fixed; surface of the pileus either scaly-excoriated or even, fibrillose, pubescent or glabrous, sometimes conspicuously rimose-lacerate but not or only short-sulcate, not long-pectinate except sometimes on drying; epicutis a trichodermium or a trichodermial palisade but tending to become fragmented into fascicles which may eventually be depressed, rarely an epithelium; volva none. On soil, sawdust, dung, tan, on decayed wood, in- and outside the woods, also on sand dunes and anthills.

*Development of the carpophores:* Probably mostly bivelangiocarpous.

*Area:* Almost cosmopolitan, but with an outstanding display of forms and individuals in tropical and subtropical America and Africa.

*Limits:* This genus is intermediate between *Macrolepiota* and *Leucocoprinus*. The absence of clamp connections in the trama of the pileus and stipe makes it possible to distinguish it from *Macrolepiota* sect. *Macrolepiota* (which is generally also well distinguishable by macroscopical characters). *Leucocoprinus* is likewise generally easy to distinguish, even macroscopically. Many of the French mycologists maintain all three genera in one (*Leucocoprinus*) but it would be difficult to maintain *Macrolepiota* and *Leucocoprinus* as independent genera unless the group of species intermediate between them, viz. *Leucoagaricus*, is admitted on the same level. The separation of *Leucoagaricus* from *Macrolepiota* and *Leucocoprinus* is not artificial at all. Those species of *Macrolepiota* without clamp connections have also some other

\*Imperfect stage of a *Leucoagaricus*. According to Decharme H. & M. Issaly (*Cryptogamie - Mycologie* 1(1): 1-18. 1980), the vegetative (imperfect) forms isolated from different species of Atta and Acromyrmex belong to the perfect form - "Lepiota" - i.e. *Leucoagaricus gongylophora* and/or related forms, see also p. 477, 478, 484.

characters which are not usual in *Leucoagaricus*. They either have excoriated, scaly, or furfuraceous pileus, or they have the annulus movable, or else they have the spores much larger than in typical *Leucoagaricus*. Usually several, but at least one of these aberrant characters is correlated with the lack of the clamp connections. Unfortunately, the clamp connections, the most decisive character, are not always easy to observe in *Macrolepiota*, and consequently, the statement that clamp connections are present or absent, must be based on very careful and time-consuming observations. In *Leucoagaricus*, so-called false clamps are occasionally observed, and may cause misinterpretations, and, on the other hand, one will always find a few clampless septa in any tissue of the species of *Macrolepiota*. Also the covering layers are often clampless in otherwise clamp-bearing species of *Macrolepiota*. It is therefore specified that the velar tissue or that of the surface layer of the stipe and the base of the basidia must be examined; especially the cotton-like inner portion of the annulus is apt to give more conclusive results than other portions of the tissue. In spite of these technical complications, the character as such is dependable and sharp - either positive or negative. It is here preferred to the characters emphasized by Locquin because *Lepiota badhamii* (considered as *Macrolepiota* by that author) and *L. meleagris* (*Leucoagaricus*) are so closely related that they are even considered as identical by some authors, e.gr. Ricken, yet, in Locquin's arrangement, they are in different subgenera (or genera). In Locquin's *Naucini* one can find all characters known in *Leucoagaricus*, and Locquin mentions their "transitional" position. In the author's opinion, they belong in *Leucoagaricus*, as emended here, excepting probably the *Macrolepiota* called *Leucocoprinus naucinus* by Locquin, but this species is not what the majority of the authors, including Fries, used to call *Lepiota naucina*, at least judging from the specimens and descriptions available.

The distinction of *Leucoagaricus* from *Leucocoprinus* appears to be simple because of the long-pectinate pileus of the latter. It is true that some species of *Leucoagaricus* have  $\pm$  sulcate or even, especially when quite mature and drying, short-pectinate margin, but the difference is generally sharp enough.

Buller's investigations on the hymenia of the agarics may eventually turn out to offer the best way of distinction between *Leucoagaricus* and *Leucocoprinus*. He states that the large species of the group *M. procerus* have hymenia of the *Panaeolus*-subtype, i.e. a subtype of the aequihymeniiferous type where the basidia are monomorphous, the pseudoparaphyses not well developed, and the spores maturing in areas alternating with other areas where the basidia are not yet sporulating. In dark-spored agarics, this arrangement causes a marbled appearance which also appears in the hymenium if first treated with iodine, preferably by Gilbert's\* method, or if very thin sections are made slicing off the hymenium of one side of the lamella, by using Melzer's reagent on the white-spored agarics with amyloid or pseudoamyloid spores. This same result was obtained by the author when fresh material of *M. excoriatus* or *L. rubrotinctus* were checked. In *Leucocoprinus* however, Buller indicated the occurrence of the *Psathyrella*-subtype (*Leucocoprinus cepaestipes*). The author found tri-to tetramorphous basidia and a short sporulating

\*Gilbert, E.J., *Emploi des vapeurs d'iode en mycologie*. Bull. Soc. Myc. Fr. 45: 141-144, 1929.

period in some of the tropical yellow *Leucocoprinini* in Florida. It may be assumed that all *Leucoagarici* belong to the *Panaeolus*-subtype, and all *Leucocoprinini* to the *Psathyrella*-subtype. However, it would be preferable to check on this character further by examining the hymenial structure of all *Leucoagarici* and all *Leucocoprinini* before this character is emphasized as the main microscopical distinction between the two genera.

Huysman (1943) has drawn attention to the fact that voluminous pseudoparaphyses are indeed present in the species of what he then called subgenus *Hiatula* sensu Heim and Romagnesi, i.e. in *Leucocoprinus* whereas these organs are absent in the *Procerus* group. For that reason he considered that *L. meleagris* and *L. badhamii* (sensu Konrad & Maublanc) are both referable to the genus *Hiatula* = *Leucocoprinus*.

Assuming that all true *Leucoagarici* behave in this regard like *Macrolepiota*, which is demonstrated only for some species, I am inclined to accept this observation as significant. The introduction of this character would make the distinction between *Leucoagaricus*, *Macrolepiota* and *Leucocoprinus* easier and more clearcut. After more species of *Leucoagaricus* have been studied with regard to Huysman's pseudoparaphyses, these characters may also become valuable for the delimitation of *Leucoagaricus*.

As for the Buller scheme, it should be noted that this *Psathyrella*-subtype of the aequihymeniiferous type does not refer to *Psathyrella* in the modern sense (as used in the present work and all contemporaneous writing) but to *Coprinus* sect. *Hemerobii* subsection *Setulosi*.

It is too early to tell whether structure of the hymenium or hymenium-type in the sense of Buller can be used as a generic character. It is quite possible that Kühner (1978) is right when he states that it is "probable that at the level of the *Leucocoprinus* [in his sense *Leucoagaricus* + *Leucocoprinus*] of coprinoid aspect one will observe, according to the species, all transitions between a hymenium recalling that of certain Coprini and a hymenium of the type of *L. procera*".

On the other hand, Kühner differentiates between two types of pores as seen in spore preparations in cresyl blue mounts. The first type in which the medulla is not colored in cresyl blue is characteristic for *Macrolepiota*, the second, where the spore is metachromatically colored purple red in its medulla, is characteristic for *Leucoagaricus* (section with distinct germ pore). This distinction of germ pore types, verified by me in several species of most groups, has supported Moser and Bon who, transferred section *Macrospori* from *Leucoagaricus* to *Macrolepiota*.

Another problem has arisen with the discovery of a species described by Singer & Digilio (*Lilloa* 25: 276. 1951, published 1952) as *Leucoagaricus exannulatus*. This species differs from both *Leucoagaricus* and *Leucocoprinus* in a poorly developed, non-persistent veil, and has a loose epithelial layer on the pileus such as can be found in *Leucocoprinus* rather than *Leucoagaricus*. But the pileus is here not splitting-pectinate, not even sulcate or striate which suggests a new section of *Leucoagaricus* with which it shares the spores which are metachromatic in cresyl blue mounts, but without a distinct apical germ pore.

I have also revised the spore characters of *Lepiota georginae* which are remarkable, as indicated by Kühner & Romagnesi (1953), because of their metachromatic endosporium, in combination with the absence of any kind of germ pore. The absence of an epithelium and of bright yellow pigments as well as the tendency to turn greenish in context and lamellae with ammonia and reddish or brownish when bruised or handled, characterizes this species as well as apparently at least three others. It became necessary, therefore, to transfer this section from *Lepiota* (and with the section *Pilosellae* Kühn.) to *Leucoagaricus* and to admit species with non-pored spores in the latter genus.

*State of knowledge:* Most species entering this genus were either little known or not known at all, even a very few years ago. Since then, the author has studied the types of several so-called *Lepiotae*, and many of these were found to be congeneric with the type species of *Leucoagaricus*. European species studied by the author at the same time were compared with the additional species transferred here to this genus. Though it cannot be claimed that all species of *Leucoagaricus* are known at present, our knowledge is adequate now in the sense that it can provide a general understanding of the outline of this genus. At present 26 species are recognized, definitely, and several more tentatively (not studied by me). The chemical characters as well as further exploration of the tropical mycoflora will extend and deepen our knowledge.

*Practical importance:* In contrast to *Macrolepiota*, few species are edible, but *L. naucinus* is sometimes used for food and sold in some markets (often confused with *Agricus* species). It has been indicated by me (1951) that the fungus (or one of the fungi) living in symbiosis with ants (Attini) - "cultivated" by the ants according to some zoologists - is an agaricaceous fungus. N.A. Weber (in several papers 1955-57) has shown that the fungi appearing in his cultures actually belong in *Leucoagaricus*, and so do some of the isolates from various ants indicated by Hervey, Rogerson & Long (*Brittonia* 29: 226-236. 1977). According to Heim (*Rev. Mycol.* 22: 299. 1957) and Singer (*Agaricales in modern Taxonomy* 3rd ed. p. 455. 1975) both Weber's and Hervey's agarics are specifically identical and congeneric with a *Leucoagaricus* which should be known as *Leucoagaricus gongylophorus* (Möller) Sing. (c.n. = *Rozites gongylophorus* Möller, *Bot. Mitt. Trop.* 6: 70, pl. I-II, 1893). A.H. Smith (in Weber) was the first to identify Weber's agaric correctly as *Leucoagaricus*. As for *Attamyces bromatificus*, Hervey et al. (l.c.) considered it as non-identical with *L. gongylophorus* because it does produce bromatia according to Kreisel, and the *Leucoagaricus* does not. Nevertheless, since some *Attamyces* isolates have a dolipore septum, and only Agaricaceae among dolipore-bearing fungi have thus far been identified as ant symbionts, it is possible that a related perfect form is still undescribed, or else that *L. gongylophorus* forms two slightly different imperfect forms.

## SPECIES

Sect. 1. *ANNULATI* (Fr.) Sing. (1972). Germ pore distinct, often narrow or non-truncate, but appearing purple red in cresyl blue mounts; spore wall smooth; spore

print white, cream, cream-orange or pink, if white, generally darkening to cream after dehydration; context either unchanging or yellowing, browning or reddening when bruised. Mostly relatively fleshy species silky surfaces which in some species tend to break up into scales, or fibrillose, to fibrillose-squamose.

Type species: *A. naucinus* Fr.

*L. naucinus* (Fr.) Sing. with the closely allied species\* *L. pudicus* (Bull. ex Fr.\*\*) Bon, *L. holosericeus* (Fr.) Moser, *L. olgae* (Vel.) Moser, and *L. carneifolia* Gillet; *L. bresadolae* (Schulzer) Bon; *L. gongylophorus* (Möller) Sing. Possibly here *Marasmius singeri* Guzmán.

Sect. 2. *RUBROTINCTI* Sing. (1948). Spores with incomplete or often absent germ pore, smooth. Context unchanging. Moderately fleshy species, with usually red, brown, pinkish ocher, olive or orange pileus; pigment mostly vacuolar.

Type species: *L. rubrotinctus* (Peck) Sing.

*L. rubrotinctus* (Peck) Sing.; *L. olivaceus* (Kauffm.) Sing.; *L. olivaceomamillatus* (Rick) Sing.; *L. confusus* (Rick) Sing.; *L. erythrellus* (Speg.) Sing.; *L. goosensiae* (Beeli) Heinemann; *L. sublittoralis* (Kühn. ex Hora) Bon & Boiff.; *L. rickianus* (Speg.) Sing. (c.n. = *Lepiota rickiana* Speg. *Bol. Acad. Nac. Cienc. Córd.* 23: 371. 1919.)

Sect. 3. *SCULPTURATI* Sing. (1972). Similar to sect. 2, but spores not smooth but with nail-like ornamentation.

Type species: *L. rubrosquamosus* (Rick) Sing.

*L. rubrosquamosus* (Rick) Sing. - In Australia and Africa apparently additional species.

Sect. 4. *LEUCOAGARICUS*. Differs from section 2 in different pigmentation on the fibrillose, ± scaly, or tomentose pileus, or else without or with little pigmentation, or pigment intraparietal, if only with intracellular pigment - pileus not bright colored; spores smooth.

Type species: *L. macrorhizus* (Locquin) Sing.; *L. atrofibrillosus* Sing.; *L. melanotricha* (Malençon & Bert.) Trimbach (unless too close to the preceding species); *L. wychanskii* (Pilát) Sing. ex Bon; *L. menieri* (Sacc.) Sing.; *L. littoralis* (Men.) Bon & Boiff.

Sect. 5. *PILOSELLI* (Kühn.) Sing. (1972). Differs from the preceding section in lamellae becoming pinkish in age and/or surfaces green with NH<sub>4</sub>OH. Spores

\*Some authors interpret *Agaricus cretaceus* Bull. ex Fr. as identical with *L. naucinus*, others with *Leucocoprinus cepaestipes*. In the sense of Fries (1821, p. 281) it is a species whose lamellae eventually become fuscous and which belongs in *Agaricus* (Psalliota).

\*\**Agaricus pudicus* Bull. (pl. 597, 2, fig. R, S, 2: 635. 1812), Fr. (a) *albus*, *Epicr.* p. 164. 1838 can be best interpreted as *Leucoagaricus*. Bull. 597, 2 L-O, b. *fulvellus* Fr. (non Bres.) is best interpreted as *Rozites caperata*, certainly not *Agrocybe aegerita* inasmuch as both "varieties" are terrestrial, as indicated by Bulliard (l.c.), not "ad trunco" as indicated by Fries. Bresadola's *P. fulvella* "Bull." is small, umboinate, with hollow stipe (in Bulliard all figures show obtuse pileus). It cannot be *A. pudicus* var. *fulvellus* Fr. and is interpreted as identical with *Agrocybe recalva* (Lasch) Sing. which is often lignicolous.

smooth, without a trace of germ pore. Context often reddening or darkening. Spore print often cream orange or pink.

Type species: *L. georginae* (W.G. Smith) Sing.

*L. georginae* (W.G. Smith) Sing.; *L. acaciarum* Sing.; *L. lilaceus* Sing. in Sing. & Digilio; probably here: *L. badhamii* (Berk. & Br.) Sing. (*Lepiota meleagroides* Huijsman) and *L. bisporus* Heinemann.\*

Sect. 6. *SPHAEROCYSTOPHORI* Sing. (1972). Epicutis of the pileus consisting of sperocysts forming an epithelium. Annulus poorly developed.

Type and only known species: *L. exannulatus* Sing.

## 125. LEUCOCOPRINUS Pat.

*Bull. Soc. Myc. Fr.* 4: 26. 1888; *Journ. Bot.*, Paris 2: 16. 1888.

Type species: *L. flavipes* Pat.\*\*

Syn.: *Mastocephalus* Batt. ex O. Kuntze, *Rev. Gen. Pl.* 2: 857. 1891.

?*Hiatula* (Fr.) Mont., *Ann. Sc. Nat.* IV. 1: 107. 1854 (vix sensu originali); *Hiatula* sensu Heim & Rom. (1934); Singer (1936).

?*Leptomyces* Mont., *Syll. Cryptog.*, p. 128. 1856.

?*Rugosospora* Heinemann, *Bull. Jard. Bot. Belg.* 43: 12. 1973.

**Characters:** Those of the tribus; habit of the carpophores much like that of the thinner *Coprinini*, a substantial portion of the pileus, at least the marginal half radially split and sulcate-pectinate, with very thin context even in the inner half; epicutis of the pileus formed by a mixture of different types of cells and hyphae, not by homogeneous palisade, also not by a hymenium; lamellae thin and soft, sometimes subdeliquescent; spore print pure white to yellowish; spores with more or less distinct germ pore, endosporium always metachromatically colored when dyed with cresyl blue, non-ornamented or rugose (in *Rugosospora*), without suprahilar appplanation or depression, or with an indistinct appplanation;; cystidia either absent, or not numerous on the sides of the lamellae; cheilocystidia usually numerous; clamp connections absent, more rarely present; tissue inamyloid; hymenophoral trama more or less regular; stipe usually with an annulus which is usually movable at least in age; cup-shaped volva none. On the earth or on various hosts.

**Development of the carpophores:** Probably always hemiangiocarpous ("bivélangiocarpique" in *L. cepaestipes* according to Reijnders 1948).

**Area:** Warmer part of the American continent, common in the tropics of both hemispheres, also often found spontaneously growing in greenhouses.

\*My collection of a certainly conspecific form had non-reddening context and slightly larger spores than the type.

\*\*If it can be proved that the publication in *Journ. Bot.* antedates the one in *B. S. M. Fr.*, the type species would be *L. cepaestipes* (Sow. ex Fr.) Pat., congeneric with *L. flavipes* Pat.

**Limits:** As for the delimitation of this genus from *Leucoagaricus*, see there. The other genera of the *Leucocoprineae* are clearly separated by the characters indicated in the key. The rare cases where some clamp connections have been observed in *Leucocoprinus* should not cause any difficulties because the other genera with clamp connections, e.g. *Macrolepiota*, are vastly different in the habit of the carpophores. Besides, the author has never found any clamps in any species, except one, later (1943) reported as *Hiatula lutea*. This is probably exceptional. However, *Rugospora ochraceobadia* (Beeli) Heinemann is reported to have clamp connections. I do not know this species. But since *Rugospora* differs from *Leucocoprinus* in the rugose spores just as *Leucoagaricus rubrosquamosus* differs from the rest of *Leucoagaricus* only in the ornamented spores, and clamp connections do occur in *Leucocoprinus*, the generic status of *Rugospora* cannot be accepted without further studies. The roughness of the spores of *Rugospora* should not be confused with the punctuation (appearing at least under the light microscope as ornamentation of type XI) of the spores of *Melanophyllum*, *Hiatulopsis*, and *Janauaria* which do not belong in the *Leucocoprineae*.

**State of knowledge:** 13 species have here been admitted. They are not distributed among sections; a possible classification has been introduced by Heinemann (*Flore illustrée Champ. d'Afrique Centrale* 5: 87. 1977).

**Practical importance:** At least one of the yellow species is violently poisonous.

## SPECIES

*L. birnbaumii* (Corda) Sing. [Agaricus, Corda; Leucocoprinus luteus (Bolt. ex Fr.) Locquin; Hiatula, Sing. 1943; Lepiota, Godfrin; Lepiota flammula (A. & S. ex aut.) Gillet; Agaricus flos-sulphuris Schnizlein; Lepiota, Mattiroli]; *P. cepaestipes* (Sow. ex Fr.) Pat. sensu str. (Lepiota, Kummer; Hiatula, Heim & Romagnesi\*); *L. cheimonocephs* (Berk. & Curt.) Sing. (c.n. = A. cheimonocephs B. & C., Journ. Linn. Soc. 10: 283. 1869); *L. lilacinogranulosus* (Henn.) Locquin (Lepiota, Henn.l.; Hiatula cepaestipes var. lilacinogranulosa Heim & Romagnesi); *L. magnusianus* (Henn. apud Rab.) Sing. (Hiatula Sing. 1943; Lepiota, Henn. apud. Rab.); *L. brebissonii* (Godey in Gillet) Locquin (Lepiota, Godey; Hiatula, Sing. 1943); *L. fragilissimus* (Berk. & Rav.) Pat. (Lepiota lichenophora Berk. & Br.\*\*); Leucocoprinus thoenii Heinemann; *L. denudatus* (Rab.) Sing. (Agaricus, Rab.; Lepiota, Sacc.; Lepiota gueguenii Sacc. & Trav.; Lepiota boudieri Guéguen non Bres.); *L. melanoloma* (Sing.) Sing. (Hiatula, Sing.); *L. bakeri* (Dennis) Sing.; *L. lacteus* (Murr.) Sing. (c.n. = Lepiota lactea Murr., Mycologia 3: 81. 1911); *L. phaeostictus* (Murr.) sensu Dennis (as Lepiota phaeosticta); *L. pluteoides* Sing. ined.; *L. venezuelanus* Dennis; obviously also *L. flavipes* Pat. & Gaill. (Hiatula, Heim & Romag-

\**A. cretaceus* Bull. p.p. (lower left figures are young Agaricus sp., the rest belongs here or to a closely related species. *L. cheimonocephs* differs in presence of spherocysts in the cuticle.

\*\*Both the original (type) collections have large spores; *L. fragilissima* sensu Heinemann & Thoen is different and probably conspecific with *L. flavipes*.

nesi); *L. spectabilis* Clemençon (*Lepiota lutea* Mattiolo non al.); *L. sulphurellus* Pegler.

## 126. SERICEOMYCES Heinemann

*Bull. Jard. Bot. Nat. Belg.* 48: 401. 1978.

*Type species:* *Lepiota serena* (Fr.) Sacc. (sensu Kühn., *Bull. Soc. Myc. Fr.* 52: 213. 1936).

*Characters:* Habit of the carpophores like that of the smaller Lepiotae with thin-fleshy pileus which may even be somewhat rimulose-pectinate, generally quite glabrous and naked but eventually sometimes developing concolorous or subconcolorous scales in age, typically quite free of pigment, i.e. white or whitish throughout; epicutis - a cutis of elongated, smooth hyphae, arranged radially, occasionally  $\pm$  gelatinized; this cutis in some species overlaid by a pulverulence consisting of spherocysts (?); hyphae without clamp connections; hymenophoral trama regular to slightly subirregular; stipe with an annulus when quite young but this may be very fugacious, without a volva; spore print white; spores with a narrow metachromatic (purple red) zone along the endosporium in cresyl blue mounts, but occasionally without a demonstrable metachromasy (see "Limits" below), generally with a minute apical disconuity (but occasionally seemingly without it, without a distinct germ pore; cheilocystidia mostly present but cystidia on the sides of the lamellae absent. On earth and humus.

*Development of the carpophores:* Probably velangiocarpous but unknown in detail.

*Area:* Widely distributed on both hemispheres in the temperate as well as in the tropical zones.

*Limits:* Since not all data on all the types belonging, according to Heinemann, in this genus are known, we follow Heinemann's cautious delimitation of his genus which appears to be well separable from the other genera of this tribus as far as the species here enumerated are concerned. However, the species with superimposed epithelium like *L. cygnea* which Romagnesi now transfers to section *Striatae* (i.e. *Leucocoprinus*) are of somewhat doubtful position. Likewise, *S. violaceus* Heinemann and some of the species inserted by Pegler in section *Sericellae* (no 4-8, 1977) are not included in the present genus as here accepted.

A further reason for me not to admit this genus in the previous editions of this work consists in the observation that certain extra-European forms otherwise scarcely distinguishable from *S. serena* have spores which do not show the metachromasy with cresyl blue which cause us now to include *Sericeomyces* in the *Leucocoprineae*. Pegler (1977, 1983, p. 348 respectively 377) finds it also absent, by implication, in his *Lepiota serena*. While these negative findings may be based on technical procedure, it is also possible that *Sericeomyces* is indeed transitory between *Leucocoprineae* and *Lepioiteae*.

The final definition of the limits of this genus will become possible when more detailed studies on more tropical species become available.

**State of knowledge:** According to the discussions under the preceding paragraphs, it is not surprising that the number of species now definitely admitted in *Sericomyces* is still relatively small. Their number will grow as further studies are carried out. In the meantime, Pegler's and Heinemann's accounts (l.c.) will be useful.

**Practical importance:** Unknown.

## SPECIES

*S. serena* (Fr.) Heinemann (sensu Kühner, non *Pseudohiatula serena* (Fr.) Sing. sensu Sing. from southern South America); obviously also *S. sericatus* (Kühn. & Romagnesi) Heinemann, *L. eriphaea* (Berk. & Br.) Sacc.

### Tribus Agariceae Pat.

*Hym. Eur.*, p. 75. 1887 (ut Agaricés); Henn. in Engl. & Pr., *Nat. Pfl.* I. 1\*\*: 230. 1898; sensu str. Konr. & Maubl., *Ic. Sel. Fung.* 6: 57. 1924.

**Type genus:** *Agaricus* L. ex Fr. sensu stricto Karst.

**Syn.:** *Psalioteae* Fay., *Ann. Sc. Nat., Bot.* VII. 9: 352. 1889 (ut Psalliotés); R. Maire, *Publ. Junt. Cienc. Nat. Barcelona* 1933: 83. 1933.  
*Psaliotoideae* (subfam. *Coprinacearum*) Sing. *Ann. Mycol.* 34: 340. 1936.

**Characters:** Those of the family; differing from the other tribus in brown, brownish purple, dull purplish red, or sepia print (if dull red - becoming so after dehydration, and blue-green or olive green when fresh); spores under the microscope never without visible pigment, either smooth (but bistratous or tristratous), or with heterogeneous wall (ornamentation of type XI, punctate when seen from above, with the upper surface in focus), sometimes somewhat unequal to subangular or even cross-shaped, with or without a germ pore, pseudoamyloid or inamyloid, never amyloid; annulus present or indistinct; volva rarely well developed; lamellae quite free, or very narrowly adnexed, rounded-adnexed or adnate (rarely so, mostly free or sub-free).

## KEY TO THE GENERA

- A. Pileus generally without a cellular or subhymeniform epicutis; spores without ornamentation and symmetrical (i.e. not irregularly subangular, never cruciform); hyphae without, very rarely with clamp connections; fresh (not dehydrated) spore print never blue-green or olive.
- B. Lamellae free.
  - C. Spores not pseudoamyloid; cheilocystidia none, or vesiculose, rarely elongated; spore print not "burnt umber" (M&P) but fuscous-brown, violet brown, sepia. 127. *Agaricus*, p. 483
  - C. Spores distinctly pseudoamyloid; cheilocystidia elongated; spore print about "burnt umber" M & P. 131. *Micropsalliota*, p. 492

B. Lamellae rounded-adjacent to adnate (see note to *Agaricus*, p. 460).

A. Pileus with a distinct epithelium or with pilose scales consisting mainly of subisodiametrical cells, or hymeniform; spores often punctulate (ornamentation type XI) or with slightly subangular outline, or even cross-shaped; fresh spore print sometimes blue-green to olive when fresh (not dehydrated); hyphae usually with clamp connections.

D. Spores punctulate with heterogeneous wall, blue-green or olive in print, becoming purple-dull red to brownish purple by dehydration, not subangular or cross-shaped; epicutis - an epithelium.

130. *Melanophyllum*, p. 491 \*

D. Spores smooth, but tending to be subangular or even cross-shaped.

E. Pileus shaggy or at least not glabrous (hand lens!), the epicutis or the spinose scales consisting partly or entirely of subisodiametrical cells; spores not cross-shaped.

F. Clamp connections present.

F. Clamp connections absent (see "C" above).

E. Pileus glabrous and naked, rugose; epicutis subhymeniform; spores cross-shaped,  $> 12\mu\text{m}$ .

128. *Cystoagaricus*, p. 488

129. *Crucispora*, p. 490

## 127. AGARICUS L. ex Fr.

*Syst. Mycol.* 1: 5. 1821; em. *Karst Bidr. Finl. Nat. Folk.* 32: xxv. 1879.

Type species: *Agaricus campestris* L. ex Fr.

Syn.: *Pratella* (Pers. ex) S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 626. 1821.

*Psalliota* Kummer, *Führ. Pilzk.*, p. 23, 1871.

*Psalliota* (Fr.) Quél., *Champ. Jura Vosg.*, p. 139. 1872-3.

*Fungus* Adans. ex O. Kuntze, *Rev. Gen. Pl.* 3(2): 477. 1898.

*Termiticola* Horak, *Sydowia Beihefte* 8: 207. 1979 (see p. 488).

*Hymenoagaricus* Heinemann, *Bull. Jard. Bot. Belg.* 51: 465. 1981 (see p. 488).

?*Singerina* Sathe & Deshpande, *Agaricales (mushrooms) of Mahar. State (MACS Monograph No. 1: 35)*. 1980.

Characters: Habit of carpophores pluteoid, reminiscent of *Leucoagaricus*; pileus naked or squamose, also with pyramidal or areolate warts, or smooth, dry, white or colored; epicutis typically (but see subgenus *Conioagaricus*) not cellular; most frequently consisting of appressed, elongate hyphae, or of fragments of a palisade; hymenophore lamellate; lamellae free but not with a collarium, eventually deep colored because of the attached spores; spore print purplish brown to "sepia" (Séguy); spores brown under the microscope, smooth, with compound wall which is not visibly pseudoamyloid, with distinct or indistinct germ pore, more often rather small than large (i.e. rarely larger than  $10\mu\text{m}$ ); basidia normal in all regards, but often consistently 2-spored, rather small; cystidia none excepting the cheilocystidia which are moderately numerous in some species, and then appear vesiculose or otherwise broad, often septate below and pedicellate, becoming obsolete in mature dried material in many cases; hymenophoral trama regular then irregular; stipe without a cellular covering, usually with a thin-membranous fugacious to thick, almost fleshy annulus and sometimes doubly annulate, and the lower annulus representing a volva which is appressed and not cup-shaped near the base; context inamyloid, often changing to reddish when bruised or changing to yellow when touched; hyphae usually without clamp connections, rarely with clamp connections

\*If spores  $> 7.5\mu\text{m}$  and carpophores volvate, see also *Metraria*, p. 512.

(?). On the soil and on dung, on tan, humus, termite nests and anthills,\* in and outside the woods. Surfaces and context of the carpophores often strongly reacting with the ordinary reagents and with a combination ("cross reaction") of anilin and nitric acid.

*Development of the carpophores:* Bivelangiocarpous; isocarpous or hymenocarpous.

*Area:* Almost cosmopolitan.

*Limits:* The color and homogeneity of the spore wall and the lack of clamp connections in the cortical layers define this genus fully. The genus *Micropsalliota* Hoehnel which was often thought to be like *Agaricus*, only smaller, has somewhat differently colored and distinctly pseudoamyloid spores. But see also note on p. 488.

*Stropharia kauffmanii* A.H. Smith and *Pholiota fulvosquamulosa* Peck, if both were actually clampless, seemed to be agaricaceous rather than strophariaceous and might, as suggested by Smith & Hesler, constitute an agaricaceous genus differing from *Agaricus* in the non-free lamellae. However, according to Redhead, *Sydotia* 37: 250-251. 1984, the former is a good *Stropharia*, the latter a good *Agaricus*. Otherwise, it is easy to distinguish *Stropharia* from *Agaricus* since the cheilocystidia and chrysocystidia in the former, in addition to the variously adnate lamellae provide a good character to separate them; also all Strophariaceae known to me have constantly and abundantly clamped septa.

*State of knowledge:* The most natural classification, it is now agreed, is the one based on the data supplied first by Schäffer & Møller (1938), and later extended by several other authors and condensed into an infrageneric classification in the first edition of the present book. In the meantime, A. Pilát, F.H. Møller, P. Heinemann, Micka, Pouzar & Svrček, Pegler and G. Bohus have made valuable contributions on the Agarici, both in Europe and in the tropics. This is a difficult and polymorphous genus and a modern world monograph would be highly desirable. At the present time, 35 species, seen by me, are recognized.

As far as *A. bisporus* is concerned, numerous data on its development and cytology, genetics, and chemistry as well as its physiology have been published. Literature on these aspects is summarized in Singer (1961\*\*), in Raper, C.A. & J.R. Raper & R.E. Miller (*Mycologia* 64: 1088-1117. 1972) and in C.A. Raper & G. Kaye, *Journ. Gen. Microbiol.* 105: 135-151. 1978. The latter paper, the most instructive one, gives comparative data on mating, fruiting, extra-cellular enzyme tests of several species of *Agaricus*. The taxonomic conclusions derived from these observations are not always fully justified since they seem to be based on the name given by many individual collectors who were not at all specialists and therefore sometimes used bino-

\*Judging from the original account which includes a photograph, the species often cited as *Rozites gongylophora* Moeller is not a *Rozites*, but has been interpreted as *Agaricus* by me; it turns out now that it is an ant-hill inhabiting species of *Leucoagaricus*. But *Locellina mazzuchii* Speg. (in reality an *Agaricus*!) also inhabits anthills regularly and other species of *Agaricus* do so occasionally. On the other hand, *Termititcola* (see below) is obviously termitophilous.

\*\*See Singer, R., *Mushrooms and Truffles*, Leonard Hill, London NW 1. 1961 (World Crops Books.).

mials which are either misdeterminations or synonyms of other species. Since identifiable herbarium specimens are not available of all stock numbers, this situation cannot always be easily corrected. The fact that the name *A. campestris* appears in three of the six groups distinguished by Raper & Kaye does reflect not on shortcomings of the present taxonomy but on the identification by the respective collectors.

**Practical importance:** Only few species slightly poisonous at times (a phenolic poisonous substance is found in *A. xanthodermus*); others are edible, and range from excellent to poor in food value. Some have been grown commercially\* e.g. *A. bisporus* (most widely used by commercial growers), *A. bitorquis* and others. The most important edible mushroom in the temperate regions of Europe and North America is undoubtedly *A. bisporus*. The production of carpophores for the food market has become a major industry, at first in France, and later in other countries. Now, according to the volume of production, the United States ranks first. Other important mushrooms growing countries are Hungary, Austria, Germany, The Netherlands, Canada, Argentina, Australia, Korea, Japan, and the U.S.S.R. In tropical countries, this species is replaced by species whose culture is cheaper because they do not need refrigeration (as *A. bisporus* does).

During the last few years it has become possible to utilize, by the application of new methods, all kinds of refuse material left over from the mushroom production for the food market, and to extract vital industrial products others than food.

The *Xanthodermatei* contain bacteriostatic substances. *A. bisporus* contains small amounts of a cancerogenic substance which is destroyed by heating.

Aside from the cultivated species, many other species are often collected by the inhabitants of various regions. Wild *Agarici* are especially in demand in Europe, all parts of Asia, especially Transcaucasia, Siberia, Indochina, China, Pakistan, Java, Japan, and the Philippines; also in Chile.

## SPECIES

**Subgenus Agaricus.** General veil not woolly or detersile and epicutis not hymeniform or epithelial.

*Type species: A. campestris* L. ex Fr.

Sect. 1. *AGARICUS* [*Bivelares* and *Univelares* Kauffman 1918 (type *P. rodmanii* and *P. campestris* respectively); *Campestres* Konr. & Maubl. (1924); *Rufescentes* Schäff. & Moell. 1938]. Context of the pileus reddening on bruising or staining brick orange, or unchanging in wounds but becoming slightly reddish in age; spores globose or ovoid-ellipsoid, always globose or nearly so in the species with reddening context; anilin oil reacting deep reddish brown on the surface of the pileus, or negative; the center of the pileus reddish to carmine with benzidin; cheilocystidia varying from practically absent to numerous, and then relatively narrow; if broadly clavate - the annulus is double or peronate and/or spores very short ( $Q = 1.3$  or smaller);

spores with or without germ pore. Species growing in open places outside the woods. General veil usually well developed, partial veil often poorly developed.

Type species: *A. campestris* L. ex Fr.

*A. campestris* L. ex Fr. (*Psalliota*, Kummer); *A. bisporus* (Lange) Imbach\* [*Psalliota*, Schäffer & Moeller; *Psalliota hortensis* (Cooke) W.G. Smith var. *bispora* Lange; *Agaricus hortensis* (Cooke) Konr. & Maubl. non Fr.]; *A. brunnescens* Peck; *A. subperonatus* (Lange) Sing. [*Psalliota hortensis* var. *subperonata* Lange; *Psalliota subperonata* (Lange) Lange; probably also synonymous or very close: *A. vaporarius* (Pers. ex Vitt.) Moser in Gams non Otto ex Krombholz; *A. campestris* B pratensis  $\alpha$  *vaporarius* Vitt.; *Psalliota bivelata* Velen. non *Agaricus bivelatus* Peck]; *A. bernardii* (Quél. apud Cke. & Quél.) Sacc.; *Agaricus bitorquis* (Quél.) Sacc. [*Psalliota*, Quél.; *Agaricus rodmanii* Peck; *A. campestris* var. *edulis* Vitt.; *Psalliota campestris* var. *edulis* Bres.; *Agaricus peronatus* Rich. & Roze; *Psalliota edulis* (Vitt.) Schäffer & Moeller; *Chitonia*, Herrfurth; *A. pequinii* (Boud.) Sing. 1938 (*Chitonia*, Boud.; *Clarkeinda*, Bres.). Probably also here: *A. solidipes* Peck, and *A. urinascens* (Schäffer & Møller) Sing. (*Psalliota*, Schäffer & Møller).

Sect. 2. *SANGUINOLENTI* (Schäffer & Møller) Sing. (1951). Characters of section 1 but growing in the woods rather than in open places and combining a slight reaction with anilin oil (on the context) with a strong reaction (slowly dark brown on the surface of the pileus) with the same reagent; core of the context purple reddish with benzidine, but cortical layer may become ultramarine; spores without germ pore; "general veil" poorly developed.

Type species: *A. silvaticus* Schaeff. ex Secr. (sensu Krombholz).

*A. silvaticus* Schaeff. ex Secr. (sensu Krombholz); *A. haemorrhoidarius* Schulz. ap. Kalchbr.; *A. langei* Møller; *A. lanipes* (Møller & Schäffer) Sing.; *A. mediofuscus* (Møller) Møller; *A. squamulifer* (Møller) Møller (as *A. squamuliferus*) (*A. caroli Pilát*); probably also *A. benesii* Pilát and *A. nebularum* Sing.

Sect. 3. *ARVENSES* Konr. & Maubl. (1924) (*Flaventes* Schäffer & Møller; *Microsporae* Lange 1926 with *P. rubella* as type species, both as sections of *Psalliota*). Carpophores tending to become yellowish or orange on pressure but sometimes unchanging; surfaces yellow or orange with NaOH or KOH, orange red or fire red with cross reaction (one streak of anilin crossed by another with HNO<sub>3</sub>, both concentrated, the discoloration appearing where the two reagents mix); core of context ultramarine (eventually almost black) with benzidine; spores without germ pore.

\*One can find in many popular articles and botanical text books the erroneous indication that the scientific name of the cultivated white mushroom is *A. campestris*, or *Psalliota campestris*. Some add that the 4-spored basidia of the wild white mushroom become 2-spored when the fungus is grown in mushroom houses, or cellars. In a careful comparative study of the macroscopical, chemical and anatomical characters of *A. campestris* and *A. bisporus* including wild forms the author has found these species to be very different, and a 4-spored *A. bisporus* would be near *A. subperonatus* rather than near *A. campestris*. It is doubtful whether the true *A. campestris* has ever been grown commercially, and it may be expected that these facts will at last be acknowledged by botanical writers. Some authors refer to the cultivated species as *A. brunnescens* Peck which is a different species (see Singer, *Mycotaxon* 20: 479-482. 1984).

*Type species: A. arvensis* Schaeff. ex Fr.

*A. arvensis* Schaeff. ex Fr. (*A. edulis* Krombh. non *Psalliota edulis* (Vitt.) Schäffer & Møller; *Pratella edulis* S.F. Gray); *A. macrosporus* (Møller & Schäffer) Pilát; *A. silvicola* (Vitt.) Peck (*Pratella flavescens* Gillet); *A. abruptibulbus* Peck; *A. augustus* Fr.; also *A. perrarus* Schulz. (if different from the preceding species), *A. projectellus* Murr.; *A. cylindriceps* Murr.; *A. pocillator* Murr.; *A. bambusigenus* Berk. & Curt.; *A. porphyrizon* Orton; *A. semotus* Fr.; *A. singeri* Heinemann.

Sect. 4. *XANTHODERMEI* Sing. (1948). Characters of the preceding section but the reaction with anilin oil × nitric acid (cross reaction) negative.

*Type species: A. xanthodermus* Gen.

*A. xanthodermus* Genevier (*Agaricus jodoformicus* Speg.); *A. placomyces* Peck; *A. endoxanthus* Berk. & Br. (*A. iodolens* Heim).

[Sect. 5. *BRUNNEIPICTI* Heinemann (1956). Differing according to its author in punctiform squamules covering the pileus, these consisting of short-celled hyphae which are ± deciduous; this is interpreted as a general veil which also occurs on the base of the stipe.

*Type species: A. brunneopictus* Heinemann & Goos.

According to Heinemann: *A. brunneopictus* Heinemann & Goos.; *A. bingensis* Heinemann; *A. kivuensis* Heinemann & Goos. - None of these known to the present author. The section seems to be very close to subgenus *Lanagaricus*, see below].

Subgenus *Lanagaricus* Heinemann (1956). General veil on the pileus woolly and/or detersile, consisting of elongated but often multiseptate hyphae.

*Type species: Agaricus trisulphuratus* Berk.

*A. trisulphuratus* Berk.; *A. crocopeplus* Berk. & Br.; *A. rufoaurantiacus* Heinemann. - Heinemann indicates 20 other species, all tropical, which are unknown to the present author and which are divided into four sections:

1. *OLIVELLI* Heinemann 1977 = *OLIVACEI* Heinemann 1956. Surface with imbricate scales; olive gray, violet or blackish. Cross reaction negative.

*Type species: A. olivellus* Heinemann & Goos.

2. *TRISULPHURATI* Heinemann (1956). Surfaces woolly; cross reaction negative; pigments yellow or red. Spores with suprahilar depression and/or endosporal thickening.

*Type species: A. trisulphuratus* Berk.

3. *RUFOLANOSI* Heinemann (1977) = *LANOSI* Heinemann (1956). As sect. 2, but pileus white, yellow, or brown, rarely red. Spores "normal".

*Type species: A. rufolanosus* Heinemann & Goos.

#### 4. LAETICOLORES Heinemann (1961). As sect. 3, but cross reaction positive.

Type species: *A. laeticolor* Heinemann & Goos.

Note: A third subgenus, *Conioagaricus* Heinemann (1956) was described as follows: "Pileus velutinous, pulverulent, or squamulose, thin at the margin and frequently striate; stipe naked or almost so underneath the annulus; elements of the pileus covering of various forms and often vesiculose or incrusted." Our own comments were (1975) "Several species of subgenus *Conioagaricus* are possibly referable to *Cystoagaricus*; at least their description does not make it clear what the differences are." Heinemann himself (1977) says: "The sectioning of the subgenus which we have proposed in 1956 has proved to be of delicate usage; we think that it must be profoundly revised. On the other hand, for many species, the structure of the pileus covering is unknown." The type species is *A. diobensis* Beeli. According to the description of that species (1956) the epicutis contains numerous spherocyst-like cells, often in chains and the septa are drawn clampless. If only species with these characteristic are admitted - and only these should be admitted - *Termiticola* belongs here, the type of which I have been able to study thanks to the amability of its author. If subgenus *Conioagaricus* is left in *Agaricus*, *Termiticola* is evidently a synonym of *Agaricus*. However, Heinemann (1980), commenting on a new section of subgenus *Conioagaricus*, viz. sect. *Hymenopilei* Heinemann (1980) says "In a future probable dismemberment of subgenus *Conioagaricus*, this section must perhaps be excluded and elevated to the rank of genus." If so, this genus should be called *Termiticola* Horak, but was eventually proposed as a new genus *Hymenagaricus* Heinemann (1981).

Whether such a genus can be separated from *Agaricus* sensu stricto with a clear enough hiatus between the two genera remains to be determined, but should be considered after full descriptions (including precise anatomical, cytological, and chemical data) of all species involved are available - an undertaking which calls for an effort on the part of specialists in tropical *Agariceae*, such as Heinemann.

Heinemann (1980 and in earlier papers) as well as myself had already separated *Termiticola* from *Micropsalliota* and *Cystoagaricus*, and so has Pegler. *Cystoagaricus* is certainly not congeneric with subgenus *Lanagaricus*, see further comments under *Cystoagaricus*.

#### 128. CYSTOAGARICUS Sing.

*Mycologia* 39: 85. 1947.

Type species: *Cystoagaricus strobilomyces* (Murr.) Sing.

Characters: Habit of the carpophores pluteoid, much like that of the small shaggy species of *Agaricus*, or else collybioid; pigment in the tissues of the cortical layers usually incrusting the hyphal walls, dark or very bright, pileus strongly convex or applanate, squarrose-spinose to subglabrous and only under a hand-lens minutely verruculose-flocculose or subfibrilllose to granular; uppermost layer of the pileus consisting of chains of subisodiametrical or ellipsoid, short-fusoid, or short-cylin-

dric cells, with few multiseptate filamentous hyphae intermixed, and these chains often subparallel to slightly interwoven and densely combined to form the ornamentalations of the pileus; lamellae free to very narrowly adnexed, ascendant or subhorizontal, moderately broad to rather broad; spore print brownish fuscous with a purplish tinge; spores under the microscope dark brownish fuscous, fuscous gray or purplish fuscous, in KOH sometimes becoming olive brown, small, up to 8.7-(9.7)  $\mu$ m long, with double wall which does not change color in Melzer's reagent (inamyloid), without a distinct germ pore, the hilar appendage not projecting but strongly eccentric, without suprahilar depression, with curved-nodose or subangular outline at least in many mature spores of the type species, somehow elongate to subisodiametrical; basidia normal, small, four-spored; cystidia and cheilocystidia pluricellular consisting of short chains of vesiculose elements and/or basidiomorphic in the form of cystidioles; hymenophoral trama regular, later subregular, stipe central, with the same kind of covering as the pileus or glabrous; annulus none; context thin, hyphae inamyloid, with clamp connections. On wood or on the ground in woods or forests, solitary, gregarious, or subfasciculate. Fig. 72, 5-7.

*Development of the carpophores:* Unknown.

*Area:* Subtropical America: Florida to Northern Argentina, also Japan and (according to Horak 1980) also in Southeast Asia, the South Pacific south to New Zealand.

*Limits:* The presence of clamp connections the typically slightly irregular outline of the spores, and absence of a distinct annulus should make it possible to distinguish this genus from the tropical subgenera of *Agaricus*. *Micropsalliotia* differs in many ways, especially in the strongly pseudoamyloid spores. *Crucispora* Horak is probably the genus most closely related to *Cystoagaricus* but can easily be distinguished by the key characters. In *Psathyrella* the lamellae are usually more broadly adnexed or adnate, and a combination of pseudoparenchymatic covering layers and septate or basidiomorphic cystidioles or cheilocystidia is never observed; furthermore, most species of *Psathyrella* have a distinct germ pore on the spores which are likewise different in shape from those of *Cystoagaricus*.

*State of knowledge:* Only three species are known.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *CYSTOAGARICUS*. Pileus and stipe pilose-squarrulose, spores, at least many of them uneven, subangular or with eccentric projections.

*Type species* (and only species): *C. strobilomyces* (Murr.) Sing.

Sect. 2. *JUJUYENSES* Sing.\* Covering of pileus reduced; stipe subglabrous; spores evenly subcylindrical, subovoid, subfuscoid.

\*Sect. n. Pileo haud piloso-squarruloso; sporis haud subangulatis.

Type species: *C. jujuyensis* Sing.

*C. jujuyensis* Sing.; *C. sachaensis* Sing.

## 129. CRUCISPORA Horak

N.Z. Journ. Bot. 9: 489. 1971.

Type species: *C. naucoroides* Horak.

**Characters:** Habit of the carpophores collybioid, pigment in the cortical layers in-crusting; epicutis sub-hymeniform; spores  $>12 \mu\text{m}$  cruciform; cystidia present; otherwise like *Cystoagaricus*. Humicolous.

**Development of carpophores:** Unknown.

**Area:** New Zealand.

**Limits:** This species and genus may well be taken for a representative of the family Bolbitiaceae. But the spores have no trace of a germ pore, rather a callus at the distal end and the spore color under the microscope is brown to sepia (some spores colored exactly as those of *Cystoagaricus strobilomyces*); the epicutis is only sub-hymeniform i.e. the cells making it up do not have their basal septa at approximately the same level. *Conocybe* sect. *Nodulosporae* has quite different spores as far as spore genesis, spore shape, pigmentation and germ pore are concerned, and it differs also in absence of cystidia and shape of the cheilocystidia, a truly hymeniform epicutis and mycenoid habit. Among the bolbitiaceous genera, one might only search for affinities with *Agrocybe* where subhymeniform epicutis and spores without germ pore often occur, and where pigment-incrustations and pleurocystidia are not uncommon. However, there is no species known in *Agrocybe* where all these aberrant characteristics are present at the same time, and there are no species which have even remotely cruciform or even gibbous spores. On the other hand, in the Agaricaceae, we know the genus *Horakia* which differs from *Crucispora* mainly in the fact that the spores become, when mature, beset with more, and more slender, excrescences and that the spore wall is hyaline, while cystidia and cheilocystidia are absent. While the two genera are not closely related, the existence of a genus with similar spore characters, hymeniform epicutis, adnexed lamellae, humicolous, shows that the approximation of *Crucispora* to *Cystoagaricus* is not arbitrary. The darker dots and fibrils on the margin of the pileus and on the surface of the stipe are likewise not paralleled in *Agrocybe* but have their counterpart in the shaggy covering of *Cystoagaricus*. On the other hand, the rugose-venose surface of the pileus is a character not unfrequently found in both Bolbitiaceae and Agaricaceae. While the present author, as well as the original one (cf. Horak, Austr. Journ. Bot. Suppl. Ser. 10: 32. 1983), does not consider the question of affinity of *Crucispora* definitely solved, he is inclined to consider *Crucispora* as agaricaceous rather than bolbitiaceous or coprinaceous since *Panaeolina rhombisperma* Hongo (Mem. Shiga Univ. 23: 38. 1973) is comparable with *P. foenisecii* rather than with *Crucispora naucoroides*, inasmuch as *P. rhombisperma* has no pleurocystidia.

*State of knowledge:* The type and only species of this genus has been restudied by me thanks to a loan by the discoverer of the genus.

*Practical importance:* Unknown.

## SPECIES

*C. naucorioides* Horak.

### 130. MELANOPHYLLUM Vel.

*Ceské Houby*, 3: 569. 1921.

*Type species:* *M. canali* Vel.

*Syn.:* *Chlorospora* Mass., *Kew Bull.* for 1898, p. 136. 1898, non *Spegazzini* (1891).

*Chlorosperma* Murr., *Mycologia* 14: 96. 1922.

*Glaucospora* Rea, *Brit. Bas.*, p. 62, 1922.

*Characters:* Habit of the carpophores pluteoid, reminiscent of certain *Lepiotas*; pileus and stipe covered with an epithelium (from the veil); lamellae free, brightly colored; spore print blue green, or olive to green (j-2 of Lange's chart), later often becoming fuscous purple by dehydration; spores under the microscope (if taken from dried material) subhyaline to rather pale umber-sepia but pigment very diluted, more concentrated only in short cylinders perforating the episporium and making the spores appear finely punctulate when the upper surface of the spores is focussed upon, ellipsoid, often angular when seen from the hilar end (the longitudinal axis of the spore pointing toward the objective) as in *Clitopilus*; without supra-hilar depression (sometimes planate), without a germ pore, hyaline when seen floating singly in water, oblong-ellipsoid to ellipsoid, rarely a central or almost central constriction in abnormal spores and then often somewhat angular but not with a subangular or wavy-nodose outline as in *Cystoagaricus*, cystidia none on the sides of lamellae; hymenophoral trama regular; stipe central, subannulate, at least the lower portion furfuraceous to shaggy from the powdery epithelium consisting of the same spherocysts as those on the pileus and filled likewise with fuscous, dissolved pigment; context fleshy, inamyloid, with odor of cucumbers; hyphae with clamp connections. On various substrata, mostly on the earth or on rotten tan, often in greenhouses, on manure piles, etc.

*Development of the carpophores:* Probably bivelangiocarpous and pileostipitocarpous.

*Area:* Europe, North and South America, East Asia, West Africa.

*Limits:* This differs from *Lepiota* with which it has been identified by Kühner and other modern authors, in having punctulate, non-pseudoamyloid spores with a very characteristic range or sequence of spore print colors. The spores are rather pale under the microscope and might be the cause of confusion with such genera of white-spored Agaricaceae as *Hiatulopsis* and *Smithiomycetes*, but the former differs

by the absence of an epithelium on pileus and stipe and the strongly radially pectinate pileus, the latter by the absence of pigment and true epithelia. *Cystoderma*, also having an epithelium on pileus and stipe, differs from *Melanophyllum* in spores with homogenous wall (non-punctate) and non-free lamellae.

*Metraria*, known only from a colored illustration and a spore print (type, K), is perhaps related to *Melanophyllum*, differing in larger spores, adnate lamellae and presence of both a volva and an annulus. Since there are no specimens available at present, the genus can not be placed with certainty, see p. 512, 609.

*State of knowledge:* Two species are completely known.

*Practical importance:* The type species has been suspected to be poisonous, but some authors go so far as to call it edible.

## SPECIES

*M. echinatum* (Fr.) Sing. (*Lepiota*, Quél.; *Psalliota*, Kummer; *Inocybe*, Sacc.; *Cystoderma*, Sing. 1936; *Psathyra*, Overholts; *Agaricus fumosopurpureus* Lasch; *Agaricus haematophyllum* Berk.; *M. canali* Velen.; *Agaricus olivaesporus* Ell. & Ev.; *Chlorosperma*, Murr.); *M. eyrei* (Mass.) Sing. (*Chlorospora*, Mass.; *Schulzeria*, Mass.; *Cystoderma*, Fayod ex Sing.; *Glaucospora*, Rea; *Lepiota*, Kühner).

### 131. MICROPSALLIOTA Höhnle

*Sitz.-ber. Ak. Wiss. Wien, math.-naturw. Kl.* 123(1): 79 [31]. 1914.

*Type species:* *M. pseudovolvulata* Höhnle.

*Characters:* Habit pluteoid, thin-fleshy to membranous, pileus silky to fibrillose; epicutis of radial hyphae, often bundled together and subascendant as in many *Agarici*; lamellae free; stipe annulate by a ± persistent but not mobile, membranous annulus; spore print fuscous brown near "burnt umber" (M & P); spores ellipsoid to amygdaliform, smooth, with homogeneous wall which is somewhat thickish, without a germ pore but often almost mucronate or with a callus, pseudoamyloid; cystidia none, but cheilocystidia numerous, generally capitate; hyphae inamyloid, without clamp connections; NH<sub>4</sub>OH provoking often (or always?) greening of the surfaces. On earth and humus.

*Development of the carpophores:* Probably hemiangiocarpous.

*Area:* Pantropical.

*Limits:* The anatomical characters together with the chemical ones have enabled Pegler & Rayner (1969) to rehabilitate this genus and to delimit it properly from *Agaricus* and *Lepiota*. The species belonging here had been formerly attached to the section *Anomalae* of *Lepiota* which is closest if the pigment of the spores is disregarded.

*State of knowledge:* Pegler & Rayner, *Kew Bulletin* 23: 366. 1969 and Heinemann, *Bull. Jard. Bot. Belg.* 50: 43-66. 1980; 53: 85-95. 1983 should be compared. Four species are known to me; two more are obviously congeneric.

*Practical importance:* Unknown.

## SPECIES

*M. pseudovolvulata* Höhnel; *M. brunneosperma* (Sing.) Pegler & Rayner (*Agaricus cephalocystis* Heinemann); *M. purpurea* Sing.; *M. cinnamomeopallida* Sing.; according to Pegler & Rayner also: *M. plumaria* (Berk. & Br.) Höhnel; *M. arginea* (Berk. & Br.) Pegler & Rayner; according to Höhnel possibly *Psalliota minima* Ricken. - Heinemann indicates 16 species more.

### Tribus Lepioteae Fayod

*Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 349. 1889 (Lepiotés) ex Ulbrich in Lindau, p. 354, 1928; *Maire, Publ. Junta Ciènc. Nat. Barcelona* 1933, p. 81. 1933.

*Type genus:* *Lepiota* (Pers. ex) S.F. Gray.

*Characters:* As in the family; spores amyloid, inamyloid, or, most frequently pseudoamyloid, with the wall hyaline, somewhat thickish, smooth or subsMOOTH, hetero- or homogenous, without a germ pore, rarely with an extremely indistinct one, without metachromatic endosporium in cresyl blue mounts, rarely with one (but then epicutis layer or repent hyphae); stipe mostly annulate perhaps also rarely with a basal volva in very few species without a veil or with extremely fugacious veil; lamellae distinctly free; spore print white, rarely cream, not changing by desiccation (excepting a slight yellowing where the print has been pure white when fresh), possibly also pale pink (?). On the ground and on living or dead host plants, even occasionally on wood, often in deep moss, etc., both in and outside the forests, but more frequently in shaded areas.

## KEY TO THE GENERA

- A. Spore wall homogeneous, smooth.
  - B. Epicutis consisting of repent, filamentous hyphae exclusively; annulus none (cf. also *Phlebonema*, p. 512); lamellae subfree (see *Pseudobaeospora*, p. 508).
    - B. Hyphae of the epicutis not consisting exclusively of repent, filamentous hyphae.
      - C. Epicutis an epithelium, consisting of spherocyst-like cells. 135. *Cystolepiota*, p. 496
      - C. Epicutis not an epithelium.
        - D. Spores pseudoamyloid, rarely amyloid or almost or (quite (?)) inamyloid; epicutis not evenly hymeniform, but in some species hymeniform on the disc, or diffract subhymeniform sections of the epicutis forming scales, or else epicutis - an (often interrupted) trichodermium or a cutis whose hyphae ascend or connive pyramidal to form fibrillose or woolly scales or furfuraceous particles on the surface of the pileus; hyphae with or without clamp connections; spore print usually white or pale cream. Development mostly bivelangiocarpous. 136. *Lepiota*, p. 497

D. Spores inamyloid; epicutis evenly hymeniform all over; hyphae with clamp connections; spore print pale cream to ochraceous. Development monovelangiocarpous.

137. *Chamaemyces*, p. 501

A. Spore wall heterogeneous and/or finely punctate or their basic shape pentagonal with broad obtuse verrucose outgrowths, later densely spinose.

E. Hyphae of the carpophore with clamp connections; epicutis not or not quite epithelial.

F. Cuticle with numerous globose or subglobose cells but not purely epithelial; spores inamyloid, with even outline, finely punctate. 132. *Smithiomycetes*, p. 494

F. Cuticle of the pileus without spherocysts; spores inamyloid or weakly pseudoamyloid.

G. Spores faintly punctate, globose or subglobose; pileus radially pectinate and lamellae free, ± remote. 133. *Hiatulopsis*, p. 495

G. Spores verruculose, not globose; pileus *Inocybe*-like and lamellae sinuate-free to adnexed (see key to Cystodermataceae).

E. Hyphae of the carpophore without clamp connections; epicutis - an epithelium; spores pseudoamyloid. 134. *Janauaria*, p. 495

## 132. SMITHIOMYCES Sing.

*Mycologia* 36: 366. 1944.

Type species: *Leucomyces mexicanus* Murr.

**Characters:** Pileus covered with extremely thin fragments of a membranous veil which consists of a tissue of heteromerous structure (spherocysts scattered among filamentous hyphae), smooth, naked except for the veil, dry; lamellae free, eroded; spore print pure white; spores hyaline, practically smooth but with a faint punctuation (ornamentation type XI) because of heterogeneous spore wall which is inamyloid, small (in the type  $5.6-2 \times 2.5-3 \mu\text{m}$ ), thin-walled (wall  $0.2-0.3 \mu\text{m}$  thick), without germ pore or callus; cystidia none; hymenophoral trama subregular, neither bilateral nor inverse; stipe central, with a distinct annulus and an inconstant, rudimentary volva which may occasionally show on the pileus as thin superimposed patches; context soft, fleshy, white (in the type species); trama inamyloid, hyphae with clamp connections. The habit of the carpophores, pluteoid, is often reminiscent of *Amanita*. On the ground in the forest, and on very decayed wood.

**Development of the carpophores:** Unknown, probably "hemiangiocarpous".

**Area:** Florida to Brazil and west to Mexico, perhaps also in Africa.

**Limits:** The key characters provide a sharp delimitation.

**State of knowledge:** Aside from the type species, a second species may possibly be congeneric.

**Practical importance:** Unknown.

## SPECIES

*S. mexicanus* (Murr.) Sing. (*Leucomyces*, Murr.; *Amanita*, Murr.; *Venenarius*, Murr.); according to the description also *Lepiota polychroa* Malençon apud Malençon & Bertault.

### 133. HIATULOPSIS Sing. & Grinling

*Persoonia* 4: 364. 1967.

*Type species: H. amara* (Beeli) Sing. & Grinling.

*Characters:* Those of the tribus; pileus with large brownish detersile scales on whitish ground, especially in the center, or with smaller verrucose scales or fine fibrils, strongly radially pectinate; epicutis formed by dense, prostrate, somewhat interwoven hyphae which form a cutis; pigments intraparietal in the epicutis; lamellae free, ± remote; spores globose or subglobose, small, symmetric, inamyloid, with firm wall (but the endosporium often metachromatic in cresyl blue mounts) which is ornamented (type XI) and heterogeneous; basidia with almost or quite straight sterigmata which at their tips bend outward to form a spiculum which bears the spore; cystidia and cheilocystidia none; hyphae inamyloid, with clamp connections; habit pluteoid, similar to *Leucocoprinus*; on woody detritus and rotten logs in tropical forests.

*Development of the carpophores:* Unknown.

*Area:* Tropical Africa.

*Limits:* *Leucocoprinus* is clearly different because of the non-heterogeneous wall of the spores; *Smithiomycetes* differs in the texture of the cuticular layer of the pileus and the absence of radial pectination.

*State of knowledge:* Only the type species is known. Pl. 84.

*Practical importance:* Unknown.

### SPECIES

*H. amara* (Beeli) Sing. & Grinling.

### 134. JANAUARIA Sing.

gen. nov.\*

*Type species: J. amazonica* Sing.

*Characters:* Habit of *Leucocoprinus*; epicutis of pileus - an epithelium (1 to several layers of globose cells with vacuolar pigment in the center of the pileus), hypodermium - a non-gelatinized cutis; cystidia inconspicuous; cheilocystidia vesiculose; basidia normal but sterigmata often curved outwards; spores very finely spinulose-punctate (appearing as ornamentation XI under the light microscope), pseudo-

\**Janauaria amazonica* gen. & spec. nov. Descriptio generico-specifica: A gen. Hiatulopside differt hyphis defibulatis; sporis cylindraceis vel ellipsoideis, appendiculo hilari excentrico, parietibus pseudoamyloideis. In Amazonia brasiliensi in vegetatione "varzea"; macroscopice Leucocoprinum confingit. Typus: Lago Janauari, Amazonas, Brasiliae, 18 III 1983, Singer B 12442 (F).

amyloid, in cresyl blue mounts no distinct metachromasy visible, without a germ pore; spore print white; stipe central, annulate, annulus non-moveable, infundibuliform; hyphae inamyloid, without clamp connections. On earth or on very rotten wood typically in inundable forest (várzea).

*Development of the carpophores:* Unknown.

*Area:* Neotropical (Amazonia).

*Limits:* This genus differs from *Hiatulopsis* in being devoid of clamp connections, and producing non-globose, non-symmetric, pseudoamyloid spores. It differs from *Leucoprinus* in the structure of the spore wall and from *Melanophyllum* in the white spore print, naked stipe, and terete spores.

*State of knowledge:* Only one species is known.

*Practical importance:* Unknown.

## SPECIES

*J. amazonica* Sing.

### 135. CYSTOLEPIOTA Sing.

In Sing. & Digilio, *Lilloa* 25: 281. 1951 (publ. 1952).

*Type species:* *C. constricta* Sing. in Sing. & Digilio.

*Characters:* Habit and appearance as in *Lepiota*. Epicutis of the pileus - an epithelium, sometimes discontinuous, consisting of subisodiametrical or isodiametrical cells (spherocysts) exclusively (these cells forming delicate floccos or a continuous subpulverulent layer); spores small, hyaline to light stramineous, with inamyloid or pseudoamyloid, homogeneous, rather thickish wall, without germ pore, not metachromatic in cresyl blue mounts, cyanophilic, typically uninucleate; hyphae of the trama with, more rarely without, clamp connections, inamyloid or weakly pseudoamyloid; lamellae free to emarginate-subfree, not remote from the apex of the stipe; veil present, but often poorly developed or fugacious; cystidia or gloeocystidia sometimes present; cheilocystidia or marginal spherocysts often present. On the ground in forests.

*Development of the carpophores:* Bivelangiocarpous and pileostipitocarpous, perhaps sometimes monovelangiocarpous.

*Area:* Known to occur in Europe, North and South America; probably also occurring in other continents.

*Limits:* It differs from *Smithiomycetes* in the configuration of the epicutis and the homogeneous spore wall; it differs from *Lepiota* section *Echinatae* in the configuration of the epicutis (which is not exclusively made up of spherocysts in *Lepiota*). Besides, in *Lepiota* the spores are generally pseudoamyloid, apparently always or

mostly binucleate, and in section *Echinatae*, spores and carpophores are larger. In *Chamaemyces* the epicutis is hymeniform.

*State of knowledge:* 23 species are well known at present.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *CYSTOLEPIOTA*. (*Lepiota* sect. *Pruinosae* Murr. 1914). Spores inamyloid.

*Type species:* *C. constricta* Sing. in Sing. & Digilio.

*C. luteifolia* Sing. in Sing. & Digilio; *C. aurantiaca* Sing.; *C. pumanquensis* Sing.; *C. rubra* Sing. in Sing. & Digilio; *C. brunneotincta* Sing. in Sing. & Digilio; *C. constricta* Sing. in Sing. & Digilio; *C. hetieri* (Boudier) Sing. (sensu Möller); *C. sisstrata* (Fr. sensu Huijsman) (*Lepiota seminuda* (Lasch) Kummer); *C. sororia* (Huijsman) Sing.; *C. australis* Sing.; *C. rosea* Sing.; *C. cinereofusca* Sing.; *C. violaceo-grisea* (Rick) Sing.; obviously also *Lepiota cystophora* Malençon & Bertault, *L. rosea* Rea, *L. adulterina* Möller, *L. cystidiosa* A.H. Smith, *L. petasitiformis* Murr., *L. luteophylla* Sundberg and *L. lycoperdoides* Kreisel.

Sect. 2. *PSEUDOAMYLOIDEAE*. Sing. & Clémençon (1972). Spores pseudoamyloid, sometimes a few spores inamyloid or (fresh) amyloid.

*Type species:* *C. bucknallii* (Berk. & Br.) Sing. & Clémençon.

*C. bucknallii* (Berk. & Br.) Sing. & Clémençon; *C. microspora* (Ellis) Sing. & Clémençon; *C. marthae* Sing. (spores very weakly pseudoamyloid); probably also *Lepiota eriophora* Peck (sensu Dennis), *L. ecitodora* Atk. and *L. purpureoconia* Atk. as well as *L. pseudogranulata* (Berk. & Br.) Sacc.

## 136. LEPIOTA (Pers. ex) S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 601. 1821.

*Type species:* *Lepiota colubrina* (Pers. ex) S.F. Gray.\*

*Syn.:* *Fusispora* Fayod, *Prodrome. Ann. Sc. Nat., Bot.* VII. 9: 351., 1889.\*\*

*Lepiotula* Maire ex Locquin ex Horak, *Beitr. Krypt.-flora der Schweiz* 13: 337. 1968.

*Morobia* Horak, *Sydotzia* Beih. 8: 205. 1979.

\*This species belongs in *Lepiota* sect. *Lepiota* and is a synonym of *L. clypeolaria*. Some authors would prefer *L. procera* as type species of *Lepiota*; however those who do so, either had to follow the American Code or selected a type species for a genus not attributed to its author, viz. S.F. Gray. The first who proposed a type species for *Lepiota* S.F. Gray were Singer & Smith (1946) who must, according to the Code of Nomenclature, be followed. Any other procedure would lead to the deplorable situation where all species of *Lepiota* would have to be transferred to *Fusispora* (see below).

\*\*This genus is described erroneously in the original diagnosis and a misdetermined species is indicated as type. Horak (1968) states that neither exsiccata nor aquarelles or sketches of the type of this genus

**Characters:** Those of the tribus. Hyphae of the epicutis not repent and filamentous nor consistently replaced by spherocysts forming an epithelium; trama of the pileus rarely (if ever) truly pseudoamyloid; hyphae with or without clamp connections; habit pluteoid but characteristic because of the presence in most species of a distinct annular veil and fibrillose scales on the surface of the pileus where a smooth disc ("calotte") is often present (where the epicutis is trichodermial or hymeniform); spores pseudoamyloid, in sect. 2 and 8 amyloid, not inamyloid (or only a few inamyloid ones among a majority of pseudoamyloid ones present), with rather thickish wall which is cyanophilic, smooth and homogeneous, without germ pore but often with more or less truncate base with or without a spur-like nodule or appendage on the outer lower side of the spore, without metachromatic endosporium in cresyl blue mounts; cystidia sometimes present but absent in a majority of the species; cheilocystidia mostly present. On the soil and on various plant débris, living or dead, such as wood, ferns, palm détritus, fiber, straw etc., not ectomycorrhizal.

**Development of the carpophores:** Probably always bivelangiocarpous and generally pileostipitocarpous. About a half dozen species have been examined (Hugueney 1966).

**Area:** Almost cosmopolitan, but the majority of the species tropical and subtropical.

**Limits:** The diagnosis given above defines the genus *Lepiota* in the narrowest and most natural sense. There are no difficulties of delimitation.

**State of knowledge:** There are undoubtedly many more species, especially in the tropics, than can be enumerated below. A monographic treatment of the genus considering essential data such as required for modern taxonomic purposes is desirable. However, a sufficient number of species - 37 - is fully known and can be distributed among the sections which are mainly based on Kühner's classification as far as this concerns the genus in the restricted sense.

**Practical importance:** None of the species of *Lepiota* is used for food in any considerable quantity nor are they sold in the markets. However, there are at least three poisonous species which may be confused with edible ones. At least one species of the *L. helveola* group (section *Ovisporae*) shows the same syndrome as *Amanita phalloides*, and apparently amanita-toxins are involved. In South America, *L. locaniensis* has been shown to be poisonous.

## SPECIES

Sect. 1. *ECHINATAE* Fayod (1889) (*Acutesquamiae* Murr. 1914; subg. *Echinoderma* Locquin). Pileus spiny or woolly-squamose, the tips of the spines often con-

(*Lepiota sistrata* sensu Fayod) are preserved; but this is not correct since *in schedulis* (G) Fayod (ined.) cancels his genus and renames the species on which it was based (naming it *Lepiota cariosa*). Since nomenclatorially *Fusispora* stands and its type is a *Lepiota* (sensu stricto), Fayod's *Fusispora* is a synonym of *Lepiota*.

sisting or, or containing, spherocysts; spores pseudoamyloid; hyphae usually with clamp connections.

*Type species: L. acutesquamosa* (Weinm.) Kummer.

*L. acutesquamosa* (Weinm.) Kummer; *L. aspera* (Pers. in Hofmann ex Fr.) Quél. (*Amanita*, Pers. ex S.F. Gray; *Lepiota acutesquamosa* var. *furcata* Kühner non *Agaricus asper* Pers. sensu Fr. 1838 which = *Amanita franchetii*); *L. asperula* Atk.; apparently also *L. microspila* (Berk.) Sacc.

Sect. 2. *AMYLOIDEAE* Sing. (1943). Pileus with woolly-spinose-squamose covering similar to that of sect. 1; spores amyloid; hyphae with clamp connections; pigment intracellular.

*L. lignicola* Karst.; *L. amyloidea* Sing. (if not too close to the preceding species\*); apparently also *Cystoderma carpaticum* Moser.

Sect. 3. *CRISTATAE* Kühner (1936). (Subgen. *Lepiotula* Locquin 1945). Cuticle of the pileus, at least on the disc, consisting of a hymeniform layer, ruptured into scales or areolae or longitudinally split over most of the remaining surface of the pileus.

*Type species: L. cristata* ("Bolt." ex Fr.) Kummer (sensu Pat.).

*L. micropholis* (Berk. & Br.) Sacc.; *L. lilacea* Bres.; *L. cristata* ("Bolt." ex Fr.) Kummer (sensu Pat.); apparently also *L. hymenoderma* Reid and five more species from Ceylon, six from East Africa (according to Pegler 1972, 1977).

*Note:* The type species of this section has spurred spores like those of sect. 4. *L. micropholis*, as *L. cristata*, has pseudoamyloid spores, but these are not spurred, and *L. lilacea* has, according to Kühner and Bon non-spurred, inamyloid or almost inamyloid spores (although material otherwise fitting the description of *L. lilacea* and determined by me as such from New York state, USA, and greenhouses in Leningrad, USSR had distinctly pseudoamyloid spores). It seems to me that the section *Cristatae* in the original sense of Kühner is too heterogeneous and should be split up. This was partially accomplished by the introduction of an additional section *Lilaceae* Bon (1981). But it is possible that *L. lilacea* ss. Kühner is closer to *Cystolepiota*. See also Horak (*Sydowia* 33: 111. 1980).

Sect. 4. *STENOSPORAE* (Lange) Kühner (1936). Cuticle of the pileus with a palisade of more or less erect hyphal elements; spores ± distinctly spurred or at least strongly truncate at the lower end.

*Type species: L. pseudofelina* Lange.

*L. pseudofelina* Lange; *L. griseovirens* R. Maire; *L. grangei* (Eyre) Lange; *L. castanea* Quél.; *L. ignicolor* Bres.; - according to Kühner also *L. subalba* Kühner ex Orton, *L. fulvella* Rea. and *L. tomentella* Lange. - *Mycena viridiflava* Rick belongs

\*The type (LE) of *L. amyloidea* Sing. is considered conspecific with that of *L. lignicola* Karst. by Knudsen and Bon; but the spores are broader and the lamellae cream colored in *L. amyloidea*.

here, and, according to Pegler (1972, 1977) three species from East Africa and five more from Ceylon; also *Morobia rhizomorphia* Horak.\*

Sect. 5. *LEPIOTA* [*Clypeolariae* (Fr.) Quél. 1872 sensu str. Kühner 1936]. Cuticle of the pileus as in the preceding section; stipe not entirely pilose, often beset with colored scales, or with the fragments of an obsolete evanescent annulus; spores not "spurred", fusoid, 8.8-16 × 4-8 µm, rarely larger, never smaller.

Type species: *L. clypeolaria* (Bull. ex Fr.) Kummer.

*L. alba* (Bres.) Sacc.; *L. metulispora* (Berk. & Br.) Sacc.; *L. ventriosospora* Reid; *L. clypeolaria* (Bull. ex Fr.) Kummer; *L. floralis* (Berk. & Rav.) Sacc.; *L. subgracilis* Kühner ex Wasser; *L. ignivolvata* Bousset & Joss.; *L. oreadiformis* Velen.; according to Locquin also *L. ochraceosulphurescens* Locquin and *L. granulopunctata* Locquin; apparently also *L. pallida* Locquin and *L. thrombophora* (Berk. & Br.) Sacc.

Sect. 6. *OVISPORAE* (Lange) Kühner (1936). Characters of the Preceding section but spores not fusoid, usually smaller than 10 µm; annulus well developed or obsolete and fugacious, usually not funnel-shaped; clamp connections present. Some or all species poisonous.

Type species: *L. subincarnata* Lange.

*L. subincarnata* Lange; *L. pseudohelvola* Kühner ex Hora; *L. felina* (Pers. ex Fr.) Karst. (sensu Quél.); *L. rubella* Bres.; *L. xanthophylla* Orton; *L. xanthophylloides* Sing. (*L. xanthophylla* Sing. non Orton); *L. locaniensis* Espinosa ("locafiensis"); *L. subcortinaria* Sing.; *L. fuscosquamula* Peck. - In addition to the above species Kühner indicates *L. parvannulata* (Lasch) Gillet, *L. citrophylla* (Berk. & Br.) Sacc. sensu aut. europ. vix Bk. & Br.; *L. setulosa* Lange; *L. kuehneri* Huijsman (as "*L. clypeolarioides* Rea"), and *L. brunneoincarnata* Chodat & Martin; Kühner & Romagnesi add what they and Huysman consider the true *L. clypeolarioides* Rea, and Locquin adds *L. barlaeana* Pat., *L. helvola* Bres. sensu Josserand, *L. rhodorhiza* Romagnesi & Locquin ex Orton, and *L. heimii* Locquin. Locquin puts *L. parvannulata* (Lasch) Gillet into a special subsection *Subalbae* Locquin where he also places "*L. erminea* aut. nonn.". This latter group is unknown to the author. Pegler (1972 indicates twelve more species (from Sri Lanka) and (1971) five more from East Africa.

Sect. 7. *ANOMALAE* Locquin (1945). Approximately same characters as in the preceding section but hyphae without clamp connections; spores pseudoamyloid.

Type species: *L. fuscovinacea* Møller & Lange; *L. neuquensis* Sing.; *L. azurea* Sing.; *L. guatopoensis* Dennis; *L. nigropunctata* Dennis; apparently also *L. plumbicolor* (Berk. & Br.) Sacc. (Pegler 1972); *L. syringa* Pegler (1977) and probably *L. rimosa* Murr.

Sect. 8. *AMYLOSPORAE* Sing. Characters of the preceding section, but spores amyloid.

\*Type material kindly provided by Horak has all the characters of the section. The lamellae of the dried specimens are not adnate but free to subfree (some perhaps narrowly adnexed).

*Type species: L. zenkeri* Henn.

*L. zenkeri* Henn.; seemingly also *L. amylospora* Malençon & Bertault which, however, belongs in *Sericeomyces* according to Heinemann.

### 137. CHAMAEMYCES Batt. ex Earle

*Bull. N. Y. Bot. Gard.* 5: 446. 1909.

*Type species: Armillaria fracida* (Fr.) Sacc.

*Syn.:* *Lepiota* subgenus *Lepiotella* Gilbert, *Le genre Amanita Persoon* p. 159. 1918.

*Lepiotella* (Gilbert) Gilbert ex Kühner & Maire, *Bull. Soc. Myc. Fr.* 50: 15. 1934; *Sing.*, *Ann. Myc.* 34: 338. 1936.

*Drosella* Maire apud Kühner & Maire, *Bull. Soc. Myc. Fr.* 50: 15. 1934 nom. nud.

**Characters:** Pileus somewhat fleshy, with hymeniform epicutis; lamellae free, but not remote (no "collarium") from the stipe; spore print pale cream to ochraceous cream (e.gr. 10-C-2, M & P); spores subhyaline, without germ pore, inamyloid, cyanophilic, binucleate, with homogeneous wall and smooth; cystidia typically present, even conspicuous on the sides of the lamellae in the type species; hyphae of the trama inamyloid, with clamp connections. On the ground and on very decayed wood.

**Development of the carpophores:** Monovelangiocarpous and stipitocarpous.

**Area:** Europe.

**Limits:** These are clear from the characters indicated in the key and in the generic diagnosis. It is not fully established whether *Lepiota rufipes* and an undescribed species from Brazil (*Mellomyces paraensis* ined., BAFC) could enter the genus *Chamaemyces* as representatives of a special subgenus. The Brazilian fungus has no clamp connections; both species have no annulus and few or no pleurocystidia; in both the color of the spores or lamellae tends somewhat to grayish or beige but the spore print was not obtained in sufficient quantity in the Brazilian species to be compared with that of *C. fracidus* and *L. rufipes*. Both species have the inamyloid spores and naked pileus and the hymeniform to subhymeniform structure of the epicutis characteristic for *Chamaemyces*. It may well be that here we have a further undescribed genus of this tribus, but its publication has to wait for fuller information on both species. *Lepiota lilacea* Bres., even if the spores are really inamyloid differs from *Chamaemyces fracidus* in several important characters, among others in white spore print and diffract pileus around a smooth center.

**State of knowledge:** With the reservation expressed in the preceding paragraph, only one species is recognized here as fully known to the author.

**Practical importance:** *C. fracidus* is edible but not very important because of its scarcity, and the low quality as food.

## SPECIES

*C. fracidus* (Fr.) Donk (Armillaria, Sacc.; Drosella, Sing.; Lepiota irrorata Quél.; Drosella, Kühner & Maire; Lepiotella, Sing.); according to Locquin also *Drosella demisannulata* (Secr.) Locqu.; according to Kühner (1978), *Lepiota rufipes* Morgan probably congeneric.

### Tribus *Cystodermateae* Sing.

*Agaricales in modern Taxonomy* 3rd ed. p. 477. 1975.

Type genus: *Cystoderma* Fayod.

**Characters:** Spores with simple or seemingly simple rather thin wall and without germ pore, smooth, or more rarely echinulate, inamyloid or amyloid, or more rarely pseudoamyloid; spore print white to ochraceous; cup-shaped volva never present; lamellae not free, but adnexed to adnate (although eventually often separating from the apex of the stipe), or rarely decurrent, consequently the habit not pluteoid although general appearance of carpophores strongly reminiscent of *Lepiota*; context consisting of hyphae with clamp connections rarely without clamp connections, and then spores strongly pseudoamyloid.

### KEY TO THE GENERA

- A. Epicutis of the pileus and covering of stipe epithelial; spores smooth or faintly ornamented; carpophores never eccentric nor rising from a protocarpic tuber.
  - B. Spore print white or nearly so; spores completely smooth, without conspicuous exo- or perisprium 138. *Cystoderma*, p. 503
  - B. Spores ochraceous in print, episporium faintly uneven, distinctly uneven under the scanning microscope but covered (excepting a suprahilar area) by a smooth outer wall-layer, inamyloid
    - 139. *Phaeolepiota*, p. 505
- A. Not combining the characters indicated above.
  - C. Spores smooth, with homogeneous wall.
    - D. Carpophores rising from a protocarpic tuber, often forming chlamydospores; hyphae with clamp connections.
      - E. Stipe with an epithelium 140. *Dissoderma*, p. 506
      - E. Stipe without an epithelium. 141. *Squamaria*, p. 507
    - D. Carpophores not rising from a protocarpic tuber and not known to form chlamydospores; hyphae without or with clamp connections; spores pseudoamyloid (if hyphae with clamp connections and spores inamyloid see *Lepioeteae*) 142. *Pseudobaeospora*, p. 508
  - C. Spores not smooth; hyphae with clamp connections; not rising from a protocarpic tuber.
    - F. Pigment intraparietal in scales; spores evenly echinulate, inamyloid, small (to 6 µm long) 143. *Ripartitella*, p. 509
    - F. Pigments intracellular; spores rounded-pentangular, their wall extended to form conic spinules, their shape often reminiscent of *Inocybe*, ± pseudoamyloid. 144. *Horakia*, p. 510

*Prodrome, Ann. Sc. Nat., Bot.* VII 9: 351. 1889.

*Type species: Agaricus amianthinus* Scop. ex Fr.

*Characters:* Those of the tribus; both pileus and stipe in the mature stage covered with a velar layer or epicutis which consists predominantly or entirely of spherocysts, forming an epithelium which may be intermixed with more elongated elements (Pl. 35); lamellae adnexed, adnate or even short-decurrent with a tooth, sometimes sinuate, sometimes separating from the apex of the stipe in age; hymenophoral trama regular to subregular (never bilateral or inverse); spore print white when fresh, perhaps sometimes pale cream; spores hyaline, smooth, with homogeneous wall, ellipsoid to subglobose, or ventricose to subrhomboid, or oblong to subcylindric, amyloid or inamyloid, rarely very weakly pseudoamyloid, binucleate and cyanophilic, rarely uninucleate and/or acyanophilic; basidia normal; cystidia sometimes present and then often reminiscent of *Melanoleuca*-cystidia; arthrospheres formed on the pileus of some species, but no chlamydospores; stipe with distinct or indistinct annulus; trama of the pileus fleshy, soft, sometimes watery, not gelatinized, inamyloid, hyphae with clamp connections. Among and on moss, on the ground in and outside the woods, more rarely on dead wood.

*Development of the carpophores:* Monovelangiocarpous; stipitocarpous.

*Area:* Almost cosmopolitan.

*Limits:* The light-spored species of *Phaeomarasmius* have a very different type of cheilocystidia and are, as far as known (Reijnders 1963) bivelangiocarpous. The veiled Tricholomas have no clamp connections but uninucleate spores, which are never amyloid and always acyanophilic; their epicuticular structure is never similar to that of *Cystoderma*. It is however remarkable that within this very homogeneous genus, we have at least one species with nodulose hilum, and that one (supposed) variety of this species (viz. *C. amianthinum* var. *sublongisporum*) has weakly to not cyanophilous spore wall (Singer 1972), whereas in *C. amianthinum* var. *rugosoreticulatum* the wall is weakly to distinctly cyanophilous, and in *C. carcharias* and *C. granulosum* cyanophilous. These data suggest that *Cystoderma*, and perhaps the Cystodermataceae are somewhat unstable and possibly transitory in spore characters. Some mycologists, including Fayod himself, also Singer (1936-43), have considered all Agaricaceae (except those with a germ pore) with epithelium as belonging to *Cystoderma*. However, Konrad & Maublanc, and later Smith & Singer emended the genus, and excluded the species with truly free lamellae and distinctly colored or distinctly pseudoamyloid spores. The genus *Phaeolepiota* which is the only other genus in this tribus with a well developed epithelium on pileus and stipe, differs in the color of the spores and in their slight rugulosity in many spore prints. *Ripartella* differs in the structure of the surface layers of both pileus and stipe, in the small, round, echinulate spores, and in the *Melanoleuca*-cystidia.

There are a few features in the species of this genus which place it at a marginal position in the Agaricaceae. Some few mycologists are inclined to transfer it to the

Tricholomataceae because of the attachment of the lamellae, the often amyloid spores, the monovelangiocarpous development, and the trama of the stipe being "confluent" with that of the pileus. Not one of these characteristics is, however, unknown in the Lepioteae and the binucleate spores which are often weakly pseudoamyloid and mostly cyanophilic, the epithelial epicutis which it shares with *Cystolepiota*, *Melanophyllum* and other true Agaricaceae refer *Cystoderma* to this latter family. Furthermore, the exclusion of *Cystoderma* from the Agaricaceae would not only exclude the Cystodermatae on nomenclatorial grounds but in view of the close relationship of *Cystoderma* with *Phaeolepiota*, *Dissoderma*, and *Squamaria* it would necessitate the exclusion and transfer of all these genera to the Tricholomataceae, and their exclusion would undoubtedly carry with it the exclusion of such Lepioteae as *Chamaemyces*. This whole subject has been treated by Kühner (1978), particularly in a special chapter (*Bull. Soc. Linn. Lyon* 47: 336 [156]-344[164]. 1978) with conclusions fully coinciding with my views. One may only add that the *Cystoderma* group has evidently no close relatives in the Tricholomataceae.

*State of knowledge:* A monographic study has been published on this genus by Smith & Singer, *Pap. Mich. Acad. Sc., Arts, Lett.* 30: 71-124, Pl. I-V. 1945. The genus can be considered as comparatively well known. 17 species are here indicated, but some more have been added by other authors recently.

*Practical importance:* Unknown.

## SPECIES

Sect. 1. *GRANULOSA* (Fr.) Locquin em. Locquin (1945), Sm. & Sing. (1945). Spores inamyloid, or sometimes extremely weakly pseudoamyloid.

*Type species:* *C. granulosum* (Batsch ex Fr.) Fayod ex aut.

*C. ambrosii* (Bres.) Sing. (*Armillaria*, Bres.); *C. subpurpureum* Smith & Sing.; *C. granulosum* (Batsch ex Fr.) Fayod ex Kühn. (*Lepiota*, S.F. Gray) and var. *occidentale* A.H. Smith apud Sm. & Sing. and var. *adnatifolium* (Peck) Sm. & Sing. (*Lepiota adnatifolium* Peck); *C. ponderosum* Sm. & Sing.; *C. granuloso-cinnabarinum* (Secr.) Sing. (*A. granulosus cinnabarinus* Secr., *Mycogr. Suisse* 1: 60. 1833; *A. cinnabarinus* Fr.; *Cystoderma* Fayod ex Konr. & Maubl.; *A. terreii* Berk. & Br.; *Cystoderma*, Harmaja; *Lepiota granulosa* var. *cinnabrina* Gillet); *C. australe* Sm. & Sing.; *C. rhombosporum* (Atk.) Sm. & Sing. (*Lepiota*, Atk.); obviously also the following (tropical) species: *C. luteohemisphaericum* Dennis; *C. cristalliferum* Thoen; *C. elegans* (Beeli) Thoen (*Armillaria*, Beeli); *C. siparium* (Dennis) Thoen (*Lepiota*, Dennis; *Ripartitella*, Dennis 1970).

Sect. 2. *CYSTODERMA* (*Amianthina* Sm. & Sing. 1945; *Genuinae* Locqu. 1945, nom. subnud.). Spores amyloid, at least in the suprahilar region.

*Type species:* *C. amianthinum* (Scop. ex Fr.) Fayod ex aut.

*C. carcharias* (Pers. ex Secr.) Fayod ex Konr. & Maubl. (*Lepiota*, Karst.); *C.*

*pulveraceum* (Peck) Sm. & Sing. (*Lepiota*, Peck); *C. caucasicum* Sing. apud Smith & Sing.; *C. amianthinum* (Scop. ex Fr.) Fayod ex Konr. & Maubl. (*Agaricus*, Scop. ex Fr.); *C. jasonis* (Cooke & Mass.) Harmaja; *C. fallax* Smith & Sing.; *C. austro-fallax* Sing.; *C. granosum* (Morgan) Smith & Sing.; *C. subvinaceum* A.H. Smith apud Smith & Sing.; *C. superbum* Huijsman\*; obviously also *C. simulatum* Orton and *C. ferruginosum* (Bres.) Pegler.

### 139. PHAEOLEPIOTA Maire

*Bull. Soc. Myc. Fr.* 27: 39. 1911 (nom. nud.) ex Konr. & Maubl., *Icon. Sel. Fung.* 6: 111. 1924-38.

*Type species:* *Pholiota aurea* (Mattuschka ex Fr.) Kummer.

*Characters:* Pileus and stipe and the underside of the broad, flaring, membranous annulus covered by a pulverulent mass which is an epithelium; lamellae adnexed; spore print light fulvous-melleous or ochraceous; spores under the microscope rather pale yellowish, pale stramineous, smooth or almost so, but under the scanning microscope with finely rugulose outer wall layer (in EM sections a continuous undulated myxosporial layer, see Capellano in Kühner, *Bull. Soc. Linn. Lyon* 47: 342, fig. 66. 1978, confirmed by H. Clémenton, pers. comm.) which - sparing out a suprahilar area - is covered by a smooth outer wall-layer (perispore?), elongate (guttiform-oblong to amygdaliform), with suprahilar depression, medium sized to large, inamyloid, cyanophilic (Pl. 51, 4-5); basidia normal in all regards; cystidia and cheilocystidia none; hymenophoral trama regular or subregular, never bilateral (excepting primordia) or inverse; stipe central, not rising from a protocarpic tuber; context thick, fleshy; hyphae inamyloid, with clamp connections; habit almost tricholomatoid. On the ground in woods.

*Development of the carpophores:* Monovelangiocarpous; stipitocarpous (Reijnders).

*Area:* Temperate zones (Europe and extratropical Asia, Western North America).

*Limits:* This genus, close to *Cystoderma* to the point of having been united with the latter by Kühner & Romagnesi (1953), has been removed from the Agaricaceae and reunited with *Pholiota* by Smith & Hesler (1968). It is indeed tempting to base such a solution on the fact that in the Strophariaceae subfamily Pholiotoideae there are species (*Phaeomarasmius*) which are annulate and have an epithelial epicutis. However, these strophariaceous species have consistently and conspicuously heteromorphous gill edge (many cheilocystidia), are bivelangiocarpous, have a different fine structure of the spore wall and a totally different habit; the spore print color may at times coincide in some *Phaeomarasmius* and *Phaeolepiota* but most or all of the former are wood- or litter-inhabiting fungi. Furthermore Singer & Machol (1971) and Machol & Singer (1972) have shown by quantitative methods that the sum of the

\*Heinemann & Thoen (1973) have proposed a third section based exclusively on this species (sect. *Superba* H. & Th., *Bull. Soc. Myc. Fr.* 89: 23. 1973) because the spores are only partially amyloid (on a suprahilar amyloid plage according to their findings).

characters make *Phaeolepiota* an agaricaceous, *Phaeomarasmius* a strophariaceous genus. A chemotaxonomical survey by Benedict & Brady and Stuntz (*Mycologia* 64: 1167. 1972) shows that the distribution pattern of urea and 10 other compounds tested chromatographically supports a relationship with *Cystoderma*, and only the distribution of one compound among eleven might suggest a relationship with *Pholiota*. This, then, confirms the opinion expressed in previous editions of the present work.

On the other hand, Pegler & Young (1971) think that *Phaeolepiota* has a suprahilar plage because the perisporium (which is smooth) covers the spore surface leaving free a suprahilar region where the spore wall proper (which appears very finely rugulose in scanning microscope photographs) is visible. However, this "plage" does not conform to the definition of plage since the suprahilar area is not less ornamented than the rest of the spore surface and is not delimited by a ragged line or more strongly pigmented rugosities forming a semicircular line around the exposed area. Since the spore wall is not otherwise similar to that of the Cortinariaceae, and cheilocystidia are absent, the conclusion that *Phaeolepiota* belongs in the Cortinariaceae near *Galerina* is not substantiated. The epithelial covering of pileus and stipe is not present in other comparable genera of Cortinariaceae; consequently, I am convinced that *Phaeolepiota* does not belong in that family but in the Agaricaceae.

*State of knowledge:* The only species referable to this genus is well known, cf. also Bach, *Dansk Bot. Ark.* 16: 1-216. 1956.

*Practical importance:* *P. aurea* is edible, at least in Europe.

## SPECIES

*P. aurea* (Mattuschka ex Fr.) R. Maire ex Konr. & Maubl. [Pholiota, Kummer; Togaria, W.G. Smith; Pholiota vahlii (Schum. ex Fr.) Lange; Lepiota pyrenaea Quél.].

### 140. DISSODERMA (Smith & Sing.) Sing.

*Sydowia Beih.* 7: 69. 1973.

*Type species:* *Cystoderma paradoxum* Smith & Sing.

*Syn.:* *Cystoderma* subgenus *Dissoderma* Smith & Sing., *Mycologia* 40: 454. 1948.

*Characters:* Those of the tribus; epicutis not an epithelium but consisting of rather irregularly arranged, mostly elongated, rarely isodiametrical elements in radial arrangement, but covering of the stipe at least at the bulb-level an epithelium (closely packed spherocysts-chains); bulb of the stipe protocarpic, with chlamydospores; basidiospores medium sized, subhyaline (spore print perhaps off white), smooth with homogeneous wall, very weakly pseudoamyloid, cyanophilic; hyphae

inamyloid, with clamp connections; cystidia none; lamellae arcuate-adnate to subdecurrent. On humus and among mosses in the woods.

*Development of the carpophores:* Unknown.

*Area:* Europe and Western North America.

*Limits:* This genus differs clearly from both *Cystoderma* and *Squamanita* being intermediate between them.

*State of knowledge:* Only one species is known. It was fully described by its authors and revised, together with European material, by Bas (1965).

*Practical importance:* Unknown..

## SPECIES

*D. paradoxum* (Smith & Sing.) Sing. (*Cystoderma*, Smith & Sing.; *Squamanita*, Bas).

### 141. SQUAMANITA Imbach

*Mitt. naturf. Ges. Luzern* 15: 81. 1946.

*Type species:* *S. schreieri* Imbach.

*Syn.:* *Coolia* Huijsman, *Medd. Nederl. myc. Ver.* 28: 59. 1943 (nomen nudum).

*Characters:* Those of the tribus; habit of the carpophores almost tricholomatoid, arising from a protocarpic tuber (often several carpophores from a large common tuber); epicutis of pileus - a cutis of parallel or interwoven hyphae sometimes bundled together and ascendant to form scales, covering of the stipe not (even at its base or on the tuber) consisting of spherocysts; lamellae ± adnate (from emarginate-adnexed or sinuate to subdecurrent); hymenophoral trama regular; spore print white or whitish (possibly darkening sometimes in contact with the lamellae); spores hyaline or subhyaline, inamyloid, weakly pseudoamyloid or amyloid, sometimes metachromatic in cresyl blue mounts according to Bas, cyanophilic, binucleate, with homogeneous smooth wall, small to medium-sized, ellipsoid, possibly also subglobose, with somewhat thickish wall when mature; basidia normal (without siderophilous granulation, mostly 4-spored); cystidia rarely present; edge of lamellae homo- or heteromorphous; hyphae inamyloid, with clamp connections; pigment intraparietal or incrusting; volva usually torn or furfuraceous to lacinate but mostly distinctly forming a universal veil of some sort, besides with an annulus or without it; protocarpic tuber more or less strongly differentiated and with clamydospore formation. On earth and humus in shady places.

*Development of the carpophores:* Monovelangiocarpous and at the same time gymnangiocarpous (the margin of the pileus is fixed to the stipe, a lisanenchym is wanting) in *S. odorata* according to Reijnders; the annular veil breaks after the

rupture of the volval tissue in *S. schreieri* according to Singer & Cléménçon. Isocarpous.

*Area:* Eastern North America and Europe; also in Japan.

*Limits:* This genus was at first inserted in the Tricholomataceae, but fuller information, provided by a paper by C. Bas (1965) and by a detailed re-examination of fresh material of the type species by Singer & Cléménçon (1972), made it advisable to transfer *Squamanita* to the Agaricaceae. This becomes even more evident when it turns out that *Squamanita* has many characters in common with *Cystoderma* and that *Dissoderma* is evidently intermediate between *Cystoderma* and *Squamanita*. The pseudoamyloid chlamydospores and the binucleate spores with cyanophilic walls confirm this conclusion.

*State of knowledge:* Bas has accepted definitively five species, one here transferred to *Dissoderma*. I am familiar with three species.

*Practical importance:* Unknown.

## SPECIES

### 1. Spores inamyloid or weakly pseudoamyloid

*S. schreieri* Imbach; *S. odorata* (Cool) Imbach ex Bas; *S. pearsonii* Bas; obviously also *S. umbonata* (Sumstine) Bas.

### 2. Spores amyloid (not known to the present author)

*S. fimbriata* Guld.; *S. contortipes* (A.H. Smith & Stuntz) Heinemann & Thoen.

## 142. PSEUDOBAEOSPORA Sing.

*Lloydia* 5: 129. 1942.

*Type species:* *Baeospora oligophylla* Sing.

*Characters:* Those of the tribus; epicutis consisting of repent, filamentous hyphae (no epithelium, no trichodermium), radially arranged; cheilocystidia and cystidia, few or none; basidia normal; spores pseudoamyloid, smooth, with homogeneous smooth wall, without metachromatic endosporium; without any trace of a germ pore; stipe central, often elongated, exannulate, lamellae subfree to adnexed; hyphae inamyloid or pseudoamyloid, typically without clamp connections. Generally on the ground, on humus, between moss thalli etc.

*Development of the carpophores:* Unknown.

*Area:* Central Asia, Europe, North and South America.

*Limits:* Kühner, Heinemann, and others insist that *Pseudobaeospora* should, contrary to Locquin's suggestion, be restricted to the original species, with the

exclusion of any species referable to *Sericeomyces*. I agree with this view. If so, the genus should be transferred as a synonym to *Collybia*, according to Kühner, but, in spite of the absence of a metachromatic spore (in cresyl blue mounts) confirmed by me in *P. pillodii* (Quél.) Horak sensu Redhead (see foot note below), I believe that the genus is better classified in the Cystodermataceae. The section *Stripedes* of *Collybia* differs strongly in appearance, pigmentation, spore print color, weaker and more inconstant pseudoamyloidity of the spores and inamyloid trama, constant presence of clamp connections, and striate to sulcate stipe, a different, non-multiseptate hypodermium, and possibly a different manner of primordial development. In the Cystodermataceae, *Pseudobaeospora* differs from all other genera in smooth, pseudoamyloid spores; in the Lepioteae, the genus could only be taken for an evelate, deteriorated form of *Lepiota*.

*State of knowledge:* At present three clampless and three clampbearing species are known. Species without clamp connections are perhaps in need of further study.

*Practical importance:* Unknown.

## SPECIES

*P. oligophylla* (Sing.) Sing.; *P. pillodii* (Quél.) Horak (sensu Horak and sensu Redhead\*); *P. defibulata* Sing.

Species with clamp connections: *P. chilensis* Horak; *P. flavescens* Sing.; *P. syringaea* Sing.

### 143. RIPARTITELLA Sing.

*Mycologia* 39: 85. 1947.

*Type species:* *Ripartitella squamosidisa* (Murr.) Sing. (= *R. brasiliensis*).

*Characters:* Habit of the carpophores reminiscent of *Lepiota* but with the lamellae variably attached, and the stipe sometimes more or less eccentric; pigment rusty, incrusting the walls of the hyphae; pileus squamulose, the squamules consisting of somewhat intermixed, dense chains of short hyphal members which are almost isodiametric to elongate and cylindric but do not assume the shape of spherocysts; lamellae adnate to emarginate or separating from the apex of the stipe, or decurrent with a tooth; spore print white or nearly so; spores hyaline, echinulate, ellipsoid to subglobose, much like those of *Clitocybe inversa*, cyanophilic, inamyloid, without

\**P. pillodii* sensu Redhead is 4-spored (as *P. oligophylla*) and has only very slightly smaller spores than those indicated by Kühner & Romagnesi (1953). *P. pillodii* sensu Kühner & Romagnesi (1954) is parthenogenetic, consequently with uninucleate spores. The spores of *P. oligophylla* are slightly smaller, strongly pseudoamyloid, and the lamellae are subdistant, whereas in *P. pillodii* sensu Kühner & Romagnesi the lamellae are close to subclose and in *P. pillodii* sensu Redhead they are medium spread i.e. medium close. It appears that the question of conspecificity of all three forms is far from being demonstrated.

germ pore; basidia normal, 4-spored; cystidioles very conspicuous in most specimens although often scarce and/or collapsed, strongly reminiscent of those of *Melanoleuca*, hyaline, thin-walled to medium thin-walled, with crystalline, sagittate incrustation above, ampullaceous or subulate, on the sides of the lamellae as well as on the edge, trama of the hymenophore regular, hyaline, consisting of thin-walled hyphae; stipe often eccentric, indistinctly or distinctly veiled but annulus rarely developed; base with short white strands of rhizomorphs (as, for that matter, in many Agaricaceae); context fleshy, consisting of hyphae with clamp connections and inamyloid walls; on the ground and on decaying wood.

*Development of the carpophores:* "Hemiangiocarpous"; details unknown.

*Area:* Subtropical and tropical America from Florida to Brazil and Bolivia; also (adventitious?) in Czechoslovakia and Hungary; also in Bonin Islands (Hongo).

*Limits:* This genus has distinctly the habit and the pigmentation of *Cystoderma*. The cystidia - though primarily reminiscent of those of *Melanoleuca* - are also comparable with the cystidia of *Cystoderma*. The general appearance is that of a *Lepiota*. It differs from other genera of Agariaceae in the characteristic echinulate spores. In this latter regard one is tempted to compare *Ripartitella* with *Ripartites*. However, *Ripartites* differs in colored spores print, in different characters of the surface of the pileus, in the lack of the cystidia, and in the mostly decurrent lamellae.

*State of knowledge:* Only two species are known. The type species has been redescribed by Singer, *Lloydia* 9: 127-128. 1946.

*Practical importance:* *R. rickenii* is edible (Futó).

## SPECIES

*R. brasiliensis* (Speg.) Sing. (*Pleurotus*, Speg.; *Marasmius squamosidiscus* Murr.; *Ripartitella*, Sing.); *R. rickenii* (Bohus) Sing.\*

### 144. HORAKIA Oberwinkler

*Sydotia* 28: 359. 1975 (1976).

Syn.: *Verrucospora* Horak, Ber. Schweiz. Bot. Ges. 77: 362. 1967 non *Verrucispora* Shaw & Alcorn (1967).

*Type species:* *Lepiota verrucosa* Beeli (= *H. flavofusca* (Henn.) Oberwinkler)

*Characters:* Habit reminiscent of *Lepiota* and *Inocybe*; lamellae sinuate-subfree to adnexed; stipe with infundibuliform, fibrous-membranous apical annulus; floculose squamules (apparently a universal veil) covering the surface of the pileus and the stipe below the annulus; spores hyaline in KOH but slightly ocher in mounts from dried material, at first rounded-rectangular or angular becoming verrucose-

\*c.n. (*Armillaria rickenii* Bohus, Bot. Közl. 57: 16. 1970).

spinulose, and (especially in the figures of Oberwinkler 1976) strongly reminiscent of *Inocybe hyperythra* but much smaller, without germ pore, weakly pseudoamyloid (Horak), not metachromatic in cresyl blue mounts (Heinemann 1973); cystidia none; cheilocystidia absent (Horak), abundant (Pegler); hyphae with clamp connections; squamules formed by short clavate to cylindric branched cells which are loosely arranged, pigment vacuolar; spore print white. On earth in forests.

*Development of the carpophores:* Unknown.

*Area:* Tropical Africa.

*Limits:* If the genus is agaricaceous, it is clearly separated from all other species of that family. However, the position of *Horakia* remains somewhat doubtful. It may be a white spored *Inocybe* comparable to the acystidiate species of subgenus *Inocybe* but the shape of the cheilocystidia as seen by Pegler, the well formed annulus, the plasmatic pigment and the weakly pseudoamyloid spores as well as the habitat (improbability of ectomycorrhiza) make this disposal of the genus unlikely. Oberwinkler (1976) claims that in spite of the white spore print, the spore shape corresponds to a high degree to that of typical Thelephoraceae which he subordinates to the order Thelephorales Oberwinkler (with "Basidiosporae... plus minusve coloratae!"). He furthermore states that Horak's genus cannot be incorporated in *Astrosporina* (i.e. *Inocybe*) because it differs in spinose spores and absence of metuloids. He considers *Horakia* an agaricoid member of the Thelephorales.

While it is certain that Oberwinkler contributed the correct generic name for Horak's genus, his further conclusions are based on erroneous statements and an overemphasis on a single character (spore shape). For the agaricologist, *Horakia* cannot be considered to belong in the Thelephorineae even if thelephoric acid were demonstrable, but as far as I am aware, no attempt at chemical analysis has been made until now.

*State of knowledge:* Only one species is known.

*Practical importance:* Unknown.

## SPECIES

*H. flavofusca* (Henn.) Oberwinkler (*Inocybe*, Henn.; *Lepiota verrucospora* Beeli; *Verrucospora*, Horak; *Verrucospora vulgaris* Pegler).

## GENERA INCOMPLETELY KNOWN

*Hiatula* (Fr.) Mont., *Ann. Sc. Nat.* IV. 1: 107. 1854. "Pileus very thin, without cuticle, formed by the interlamellar hypophylloous tissue (e dorsis lamellarum juncitis formatus) as in the thinnest *Coprini*, but not deliquescent, and spores white". Fries,

*Nov. Symb.*, p. 27, *Hiatula*, subgenus *Agarici* (1851). The type species is *Agaricus (Hiatula) benzonii* Fr. See p. 846.

*Leptomyces* Mont. *Syll. Crypt.*, p. 128. 1856. The type, *L. lignifragus* (Mont.) Mont., gives the impression to be congeneric with *Hiatula*. See also p. 847.

*Metraria* Cooke & Mass. apud Sacc. 9: 82. 1891. "Stipe central; volva and annulus distinct; pileus fleshy; spores flesh color. Analogous with the genus *Amanita*". Saccardo. The type species is *M. insignis* Cooke & Mass. apud Sacc. For the longest time, there was no trace of the material, but in 1954 this writer was able to unearth among Cooke's original paintings not only the original drawing of the species but, in addition, a spore print, now inserted in the herbarium. A study of the spores of *Metraria* reveals that the genus has no close affinity with the Pluteaceae or the white-spored Amanitaceae. These spores, rather unique among gill fungi spores, are  $8-10.3 \times 5.8-7 \mu\text{m}$  ovoid, inamyloid, not metachromatic in cresyl blue mounts, with a thin endosporial layer; the episporium smooth in outline but very conspicuously heterogeneous consisting of ochraceous brown spinules inserted in pale pink wall substance (type XI of spore ornamentations in Basidiomycetes), consequently spores appearing punctate when the upper surface is focussed upon, without germ pore and without suprahilar depression (Singer, *Sydowia* 9: 400. 1955). The color of the spore print is now between "ferruginous" and "hazel" (Ridgway) and this is probably the same color as had been observed when fresh since the spore dusting as painted in the original painting (Martin no. 561) shows the same tone. The spore surface appears smooth in SEM view.

If it is admitted that the spore print belongs to the original painting and is of Australian origin, the genus belongs most probably in the Agaricales, Agaricaceae, or perhaps the Cortinariaceae. There is, however, no proof that this is actually the case, and the type species has, under the assumption that the spore print was added later from different material, been tentatively considered to belong to *Amanita*, whereas the spore print is said to belong to *Hebeloma*. For further comment see under *Hebeloma*, p. 609.

*Phlebonema* Heim, *Compt. r. Acad. fr.* 188: 1567, 1929. "Carpophore fleshy, not hygrophanous, with initially incurved margin, with .... glabrous, non-viscid cuticle; stipe not separable from the pileus, solid; lamellae completely free, numerous, broad; flesh white, intensely staining yellow when bruised, formed by hyphae which are all more or less vascular; spores (in mass) pale ocher, (under the microscope) small ( $5.5-6 \times 4-4.5 \mu\text{m}$  in the type species), smooth, subtetragonal in outline, with a large suprahilar appplanation, without germ pore, with distinct and small hilar appendage; basidia clavate-elongate, tetrasporous; cystidia none, edge of the lamellae homomorphous; on the earth." Heim. The type species is *Phlebonema chrysotingens* Heim, a species described by Heim from Madagascar. It has a cutis on the pileus, consisting of filamentous hyphae which are illustrated in "*Le Genre Inocybe*", Paris 1931, p. 60, Fig. 98, A. Here, the septa are drawn clampless; the spores are said to consist of a hyaline episporium and brown endosporium (which is rather unusual). The context consists entirely of conducting elements (l.c., Fig. 98C), and toward the cuticle more and more ordinary hyphae are intermixed (Fig. 98B).

The author has not seen the type which has been lost, but it seems rather obvious that this species has no close relatives in the Strophariaceae, or for that matter in any ochrosporous group. The description impresses one as suggesting a species of the family Agaricaceae (*sensu nostro*), and it would be interesting to check on the behavior of the spores of *Phlebonema* in cresyl blue, in the Melzer reagent, etc. As Horak correctly observes (1968, p. 458), the problem of its precise position can, unfortunately, only be fixed on hand of new collections. These, especially if coming from Maromandia (type locality), might then serve as neotypes. *Psalliota dialeri* Bres. & Torrend may be congeneric.

*Pilosace* (Fr.) Quélet, *Chmp. Jura Vosg.* 2: 360. 1873 (*Agaricus* subgen. *Pilosace* Fr. *Nov. Symbol.*, p. 25. 1851). "Pileus distinct from the stipe (Hymenophorum a stipite discretum); lamellae free and in the first species [*A. tricholepis* Fr.] remote from the stipe as in *A. procerus* [*Macrolepiota procerula*]; spores fuscous; veil none; nearest to the *Psalliotae* [*Agaricus* *sensu Karst.*] but without any veil..." Fries. The type species is either *A. tricholepis* or *A. hololepis* Fr. The author prefers the latter as a lectotype. Both species are based not on specimens but on figures of very doubtful value. Quélet has added a new element in describing another species in this genus, *P. algeriensis*. What this actually is, cannot be said with certainty, and even the French mycologists have only hypotheses on this subject. But even if the position of this species could be cleared up, the status of Quélet's species would have no influence on the status of the genus *Pilosace* as such. Some of these species might be exannulate *Agarici*, and this is the reason why *Pilosace* is mentioned here.

*Schinzinia* Fayod, *Verh. Bot. Ver. Brandenburg* 31: 227. 1890. "Characters of *Pluteus* but with tough consistency" Fayod. The type species is *S. pustulosa* Fayod from East Africa. The abbreviated description above does not give an impression of the affinities of this species. The good figures published by Fayod (*l.c.*, Pl. 3) leave no doubt but that this is a genus of the Agaricaceae since the spores are double-walled and conspicuously apiculate. However, there is no indication on the clamp connections, and besides the metachromasy of the spore wall in cresyl blue is not known. Even so, the genus *Schinzinia* might be recognized as valid were it not for the fact that the material comes from an exotic region where it had been collected by a non-mycologist. The movable annulus of the *Leucocoprineae* tends to fall off dried specimens, and it is almost probable that *Schinzinia* is just such a mutilated *Macrolepiota* or more probably *Leucoagaricus*. Africa is very rich in species of *Leucocoprineae*, some of them with pink spores. Unless more good material from the type locality is examined, it is felt that *Schinzinia* should not be admitted on the same level as *Macrolepiota* and *Leucoagaricus*. Heinemann (1956) identifies (with a question mark) *Schinzinia* with *Agaricus* subgenus *Lanagaricus*.

*Schulzeria* Bres., *Schulzeria, Nuov. Gen.*, p. 7. 1886. "White spored agarics without volva and annulus; lamellae rounded behind, free, remote; spores obovate, hyaline. (Exannulate Lepiotas or white spored *Plutei* or *Pilosaceae*)" Bresadola. The type species is *S. rimulosa* Schulzer & Bres. apud Bres. from Yugoslavia. The pictures and the original description published by Bresadola are taken from the original illustration and notes by Schulzer; consequently Bresadola had no other

part in it than to publish the material under a new generic name. One of Bresadola's comparisons, viz. "*Lepiotae* without annulus", seems to be most characteristic for the fungi in question. If the data published could be taken at their face value, it might certainly be possible to speak of a genus close to *Lepiota* but without annulus. However, it is not quite certain that Schulzer's spore measurements were correct. The small spores without a germ pore would exclude Leucocoprineae. It may be assumed that Schulzer overlooked the germ pore if one was present. As for the veil, its complete absence in specimens of the size of these Schulzerias would undoubtedly be remarkable were it not for the fact that it may have been overlooked because the specimens were too old, or because the annulus mobilis had slid down the stipe without having been noticed by Schulzer. Schulzer's own publications are not always reliable as far as exactitude of observation is concerned, and the same shortcoming may be attributed to the material sent to Bresadola. Since there is at present no way to prove either the correctness or the faultiness of Schulzer's observations, the genus *Schulzeria* is here listed as incompletely known, yet the author tends to believe that it refers to a mutilated, misrepresented *Leucoagaricus* or perhaps *Lepiota* rather than an autonomous genus of the *Lepioeteae*.

## COPRINACEAE Roze

*Bull. Soc. Bot. Fr.* 23: 51. 1876 (*nom. nud.*); *l.c.*, p. 111. 1876 (ut Coprinidées); *Van Overeem in Van Ov. & Weese, Icon. Fung. Malay.* 6: 3. 1924.

Type genus: *Coprinus* (Pers. ex) S.F. Gray.

Syn.: *Scotosporaceae* Romagnesi, *Rev. Mycol.* 2: 23. 1937 (*nom. nud.*).

*Zerovaemycetaceae* Gorovoy, *Dokl. Akad. Nauk Ukrainsk. SSR*, 8: 746. 1977.

**Characters:** Hymenophore lamellate; the lamellae of the *Coprinus*-type (with parallel or subparallel sides) or wedge shaped, of the aequihymeniiferous or the inaequihymeniiferous type; in the genera with aequihymeniiferous and wedge-shaped lamellae - epicutis of the pileus always characteristically cellular, the epicutis often consisting of somewhat compressed (not always quite globose) but distinctly subisodimetric bodies which are often somewhat colored, or arranged in chains but not mealy in most species, rather rarely covered up by a velar layer which consists of elongate elements; otherwise, i.e. if the lamellae are of the inaequihymeniiferous type or with parallel or subparallel sides, they usually tend to deliquesce, and in extreme cases which are rather common, the whole pileus eventually deliquesces, the drops formed being black in the majority of cases, more rarely fuscous, etc. (according to the color of the spores in mass), and white in sterile specimens; spores, where obtainable in print, usually dark colored: black, dark fuscous, purplish fuscous, rarely as light colored as dull purplish lilac or russet-lilac, or brick-russet; individual spores rather dark colored under microscope in most species, more rarely light colored, usually with distinctly double or even more complex wall, with, rarely without, a well developed germ pore, smooth, rarely warty, echinate, reticulate or otherwise ornamented, globose, ellipsoid, cylindric-oblong, almond-shaped, lemon-shaped, angular, the smaller diameter (breadth) usually equal in all positions, more

rarely compressed as in many *Psilocybes* (*Deconica*), rather small to very large, sometimes in different sizes according to the age-group of basidia from which they were discharged, normally binucleate, hilum of the open-pore type; basidia normal but rather short and broad in many species; lamellae free to subdecurrent, in the species without volva and with non-deliquescent lamellae never quite free; hymenophoral trama regular, becoming subregular in age; stipe central, with or without veil; context fleshy to membranous, often very fragile; tissue consisting of hyphae with or rarely without clamp connections. On various substrata, frequently on the earth, or on humus, or on dead wood, or on dung, or on fallen leaves, or on sand, in and outside the woods, often in buildings, in greenhouses, etc., even parasitically on other agarics or on various Cormophytes.

**Limits:** The *Coprinaceae* are here restricted to the three subfamilies *Coprinoideae*, *Psathyrelloideae*, and *Panaeoloideae*. These three subfamilies as a unit, are very natural and closely related to each other. They differ from all the other dark-spored agarics by either having the *Coprinus*-type of hymenophore or having a cellular epicutis. Aside from that most normal forms have clamp connections, and the spores are usually provided with a germ pore and are dark (not bright colored or pale) in a good print. In fact, it appears that the *Coprinaceae* are more closely related to the *Agricaceae* and the *Bolbitiaceae* than to any of the other dark-spored groups. As for the delimitation of the *Coprinaceae* from the latter two families, the reader is referred to the corresponding paragraph under the *Agariceae* and under the *Bolbitiaceae*.

#### KEY TO THE SUBFAMILIES

- A. Sides of the lamellae parallel or subparallel; pileus often deeply plicate at least near the margin; hymenophore and margin, or even the whole carpophore, mostly deliquescent. *Coprinoideae*, p. 515
- A. Lamellae more or less wedge-shaped in cross section, i.e. acuminate toward the edge, the sides not parallel, non-deliquescent.  
B. Spores discolored with concentrated  $H_2SO_4$  to pale slate color, even if they were black and opaque when seen in water. *Psathyrelloideae* (but cf. *Coprinoideae*, if pileus deeply grooved-plicate), p. 523.  
B. Spores not discolored in  $H_2SO_4$ . *Panaeoloideae*, p. 533

#### Subfamily *Coprinoideae* Henn.

In Engler & Prantl, *Nat. Pfl.-fam.* I. 1\*\*: 204. 1898 (ut *Coprineae*, subfam. of Agaricaceae); (Fayod) Sing., *Ann. Mycol.* 34: 339. 1936 (ut *Coprinoideae*, subfam. of *Coprinaceae*).

**Type genus and only genus:** *Coprinus* (Pers. ex) S.F. Gray.

Syn.: *Coprinoideae*, Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 379. 1889 (ut subtribus).

*Coprineae* (Fayod) Heim, *Treb. Mus. Ciènc. Nat. Barcelona* 15: 132. 1934 (ut tribus).

**Characters:** Sides of the lamellae mostly parallel (Pl. 22); hymenophore of the inaequihymeniferous type; epicutis not always cellular, often in hyphal chains, or merely radially-fibrillose, or with a dichophysoid structure, etc.; hyphae with, or

more rarely without clamp connections (probably all "normal" i.e. heterothallic tetrasporous races, with clamp connections, but the species very variable in their sexuality). On the soil, or on various other substrata.

#### 145. COPRINUS (Pers. ex) S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 632. 1821.

*Type species:* *C. comatus* (Müller in Fl. Dan. ex Fr.) S.F. Gray.

*Syn.:* *Prunulus* Ces. ex S.F. Gray, l.c., p. 630.\*

*Onchopus* Karst., *Bidr. Findl. Nat. Folk.* 32: xxvii. 1879.

*Pselliphora* Karst., l.c.

*Coprinellus* Karst., l.c.

*Coprinopsis* Karst., *Hymenomycetes Fennici, Acta Flor. faun. Fenn.* 2(2): 27. 1881.

*Oncopus* Karst., *Basidiv.*, p. 256. 1889 (spelling variation of *Onchopus* Karst.).

*Lentispora* Fayod, *Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 379. 1889.

*Ephemeroxybe* Fayod, l.c., p. 380.

*Annularius* Roussel ex Earle, *Bull. N.Y. Bot. Gard.* 5: 443. 1909.

*Pseudocoprinus* Kühner, *Le Botaniste* 20: 155. 1928.

*Ozonium* Link ex Fr., *Syst. Myc.* I: Ivii. 1821 (Mycelia sterilia, not priorable).

*Rhacophyllus* Berk., *Journ. Linn. Soc., Bot.* 11: 559. 1871. (*Rhacophyllus* form of *Coprinus clastophyllus*).

?*Zerovaemyces Gorovoy, Dokl. Akad. Nauk. Ukr. SSR* 8: 746. 1977.

**Characters:** Pileus usually conical or campanulate in youth, more rarely initially subglobose, then expanding in many species, especially in the small ones; structure of the epicutis and velar layers very varied; margin (or often the entire pileus except for the narrow disc) frequently deeply plicate-furrowed along the back of the lamellae which generally, (but see "Limits" below) have parallel sides (Pl. 23) and mostly (not always in sect. *Hemerobii*) disappear in age by autodeliquescence starting from the edge upwards, free or sinuate, or adnexed, or adnate; hymenium consisting of isolated basidia (Pl. 24,2) arranged rather regularly according to stage of development among sterile cells - pseudoparaphyses - and thus offering a checkerboard-like aspect when looked at under low power at the time when the spores begin to mature; characteristic large cystidia (trabecular cystidia, "Balkenzystiden" Van Overeem), very frequently present on the sides of the lamellae (Pl. 23); cheilocystidia proper not differentiated in most species but the edges of the lamellae often heteromorphous because of the presence, there, of large loosely attached sphaerocysts; spore print black or fuscous; spores under the microscope blackish and opaque (Pl. 24,2), more rarely fuscous and opaque, or transparent, but always very deeply colored by a pigment which can easily be extracted and destroyed by concentrated sulphuric acid, leaving the spore wall pale slate color, with germ pore, smooth, more rarely warty, echinate, reticulate, or angular frequently compressed from both the inner and outer side to become approximately lentiform as *Psilocybe*

\*The earliest selection - *A. extinktorius* Sow. - made independently of the first-species rule is that by Singer & Smith (1946); this selection is based on the incompatibility of the generic description with the naked pileus of *P. denticulatus*.

sect. 6, axially asymmetric and sometimes almost completely asymmetric, with complex wall, the perisporium often comparatively persistent; basidia normal but rarely clavate, usually - cylindric or even narrowed in the middle, (1)-2-(3)-4-spored; hymenophoral trama regular; stipe central and more or less straight; veil present or absent, and, if present, often indistinctly double, often condensed into an annulus, or with an annulus in the lower part of the stipe and the veil then resembling a volva, usually also apparent on the pileus (floccons, etc.), rarely with a true, well developed cup-shaped volva at the base; context usually white or whitish, fleshy, or very thin and fragile to almost absent in the tiniest species and specimens; clamp connections more often present than absent, and perhaps always present in the normal forms. On dung, or on soil, sand, peat, on various fabrics, on living Basidiomycetes, around living tree trunks, on dead wood, etc., also in buildings, often in greenhouses, on charcoal, in and outside the woods; often forming small sclerotia.

*Development of the carpophores:* Mostly or always "hemiangiocarpous"; for more details see the comprehensive paper by Chung Hwang Chow, *Contribution à l'étude du développement des Coprins. Le Botaniste* 26: 89-236. 1934, also Atkinson (1916), Levine (1914), Kühner (1926), and Reijnders (1948, 1952, 1963, 1979). Reijnders indicates the following types of hemiangiocarpy in different species of the genus: Gymnangiocarpous (*C. plicatilis*); paravelangiocarpous (few species); bivelangiocarpous (most species). According to Watling (1985) 41 species have been analysed.

Reijnders (*Persoonia* 10: 383-424. 1979) has given a comprehensive survey of the ontogeny of the genus which is one of the most thoroughly studied groups in this respect (with about 27 species examined). All species have a strong concentration in the primordial state; they are pileostipitocarpous, isocarpous, or pileocarpous, and the stipes remain short for a long time. The stipe formation in its earliest stages is sometimes indistinct because of the longitudinal direction of the hyphae from the beginning. The universal veil is versiform as far as structure is concerned and often contains special cells e. gr. spherocysts, or has been dissolved into peculiar hairs, or is wanting in cases where a "hymenoderm" (a hymeniform epicutis) is developed. The development of the lipsanenchyma is also subject to variation. Though it is present in most cases, it is often scanty, yet, sometimes, it is abundant. Most of the species are bivelangiocarpous. Many are paravelangiocarpous if the peculiar hairs of the surface are not considered a universal veil. The species of section *Hemerobii* are gymnangiocarpous. The ruphymenial type of gill formation is frequent in *Coprinus* and there are many transitorial structures between this mode and the normal one (by folds).

The *Rhacophyllus* forms now known to be linked with *Coprinus* are probably bivelangiocarpous and generally hymenopileocarpous or isocarpous (see also Reijnders & Malençon 1969).

In the case of *Coprinus*, the ontogenetic data are highly correlated with the sections here adopted which is not surprising since they are largely based on the characters of the veils.

Reijnders has also made an attempt at elucidating the phylogenetic relations within the genus *Coprinus* and discussed the question which of the characteristics should be considered primitive.

*Area: Cosmopolitan.*

*Limits:* The autodeliquescence of the lamellae is mostly quite obvious where true *Coprinini* grow under optimal conditions. This, combined with the peculiar type of hymenophore and hymenium should make it rather easy to distinguish *Coprinus* in most cases.

Whether to include in *Coprinus* the genus *Pseudocoprinus* Kühner (non-deliquescent) remains at the present time the only problem of delimitation open to discussion. On the basis of the data presented by Kühner the present author has accepted the fact that both Buller and Kühner coincided in the interpretation of the morphological and developmental features of *Coprinus disseminatus* as showing that this species is not a typical *Coprinus*; the manner of formation of the hymenial ornamentation by folding always ends up in wedge-shaped transversal section in adult specimens which would be in contrast to the development of typical *Coprinini*. Nevertheless, Romagnesi who has accepted Kühner's genus in 1936, abandoned it in a later paper and both Morten Lange and Kühner & Romagnesi insist now on the generic identity of *Pseudocoprinus* with *Coprinus*. This author, who has not participated in the research on this interesting problem, does not feel competent to reaffirm his earlier inclination to accept the genus *Pseudocoprinus*, and includes it now in *Coprinus*. This does not mean that a future reorganization of the genus *Coprinus* - as far as its infrageneric taxonomy is concerned - might not lead to a second reappraisal of the situation with a taxon containing the genus *Pseudocoprinus* appearing with a new circumscription and possibly at a higher level than the subsectional one (subsect. *Setulosi*) where *C. disseminatus* is placed now.

There cannot be any doubt now that *Rhacophyllus* is a synonym of *Coprinus*. It is tempting to think that the same might be true as far as *Zerovaemyces* is concerned. See also p. 19, 857.

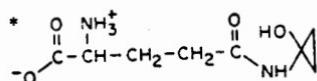
*State of knowledge:* The best and most modern treatments of the genus are found in keys to and monographs of European species, particularly Kühner & Romagnesi (1953) and Orton & Watling, Coprinaceae part 1 in: British fungus flora, agarics and boleti, Henderson, Orton & Watling, eds.). Unfortunately, comparable works based on extra-European fungus floras have not come to this author's attention, and even the accounts on European species do not seem to be complete. The reason for this situation may well be found in the somewhat different methods of collecting and preparing and the desirability of cultivating the material collected. The abundant experimental work which has contributed to the knowledge of the taxonomy of the genus has not always been coordinated with the modern taxonomical work, especially in the Americas.

This author does not feel competent, in view of the enormous number of species that must exist, to provide a representative survey of the species of the different sections and subsections. There are undoubtedly several hundred species in the

world and a comparison of Morten Lange's recent work with the treatment the genus has been given by Kühner & Romagnesi suggests that the somewhat over 70 species indicated and keyed out by the latter authors do not include all European species either. Orton & Watling (1979) describe 91 species for Great Britain alone. We have therefore maintained the same policy as was followed in the first edition of the present work and reduced the enumeration of the species to a bare minimum of 43 representative species personally known to the author. This treatment will provide a general orientation but the reader is referred to the important taxonomical, cytological and experimental work quoted in the literature list, particularly Kühner & Romagnesi (1953), Morten Lange (1952), but also Buller, Vandendries, Quintanilla, Chung Hwang Chow, and some scattered contributions by various authors such as Josserand, Boedijn, A.H. Smith, Romagnesi, etc.

Especially valuable is the work by Morten Lange ("The species concept in the genus *Coprinus*") who was able to show that in subsect. *Setulosi* and probably generally in *Coprinus*, species with seemingly insignificant though inheritable morphological characters do not form hybrids with related forms; even some seemingly morphologically homogeneous strains can be separated into mutually incompatible strains. He established the fact that species differing from related ones apparently exclusively by the number of spores per basidium, remain constant and are specifically distinct. Whether this latter conclusion is applicable in this family generally, or merely in the subsect. *Setulosi* of *Coprinus* is not fully established. Nevertheless, the experience collected in *Agaricus*, *Conocybe* and *Mycena* indicates that the situation in *Coprinus* cannot be generalized for all Agaricales.

**Practical importance:** The *Coprinini* are easy to cultivate under usual laboratory conditions and therefore lend themselves better than most other agarics to all kinds of investigations, demonstrations and for a potential use in industry. It is unfortunately impossible to grow them for food because of the difficulty of transport. Their early autodeliquescence makes it practically impossible to have them in the market before they are "inky". However, several species are harvested by amateurs every year as long as they are very young, and are considered as first class edible mushrooms. In this category belong especially *C. micaceus*, *C. comatus*, and *C. cinereus*. *Coprinus atramentarius* is of lesser quality as far as taste is concerned. Lindberg, Berkman & Wickberg (*J. C. S. Chem. Comm.* 94: 6-947. 1975) indicate the physiologically active substance in carpophores of *C. atramentarius* (40mg in 1 kg) - coprine\* - and thus corroborate the observations by French mycophagists who claimed that it is unwholesome, causing erythremia, if consumed before or after alcoholic beverages although A.H. Smith thought that, at least in America, *C. insignis* Peck, not *C. atramentarius*, is the poisonous species. *C. atramentarius* is the main source of what is known as *Coprinus* ink, a suspension of the spores in water and several other ingredients. It has approximately the properties of Chinese ink,



(Hatfield & Schaumberg, *Lloydia* 38: 493. 1975.)

and is used for retouching work in photography, and in emergencies and for specific effects, in writing and drawing. The *Coprinus* ink has some future in police work since a given mixture of species would provide an easily recognizable ink in documents of importance.

Certain species of *Coprinus* are known to be "weed fungi" in the manure beds prepared for mushroom growing. They develop faster than the *Agaricus* and appear before the first fruiting bodies of the latter can be harvested, sometimes even on the fermenting manure heaps before they are taken into the mushroom houses or cellars. Their influence on the production of carpophores by the *Agaricus* has been interpreted in different ways by different growers. The word "weed fungi" would imply a certain degree of competition for nutrition in the substratum, and a certain damage done to the mycelium of the *Agaricus* since it is deprived of optimum conditions long before it reaches the stage of fructification. On the other hand, practical experience shows that growers do not dread the appearance of the *Coprinus*, on the contrary, they are usually taken as a sign that the quality of the manure is good, and a normal harvest can be expected. A scientific approach to this problem would be desirable in the interest of the mushroom industry.

Some of these normally dung-inhabiting and sometimes straw-inhabiting (and occasionally "weed")-species have recently been cultivated and proposed to be merchandized in their own right, as edible mushrooms (Kurtzman Jr. in Chang & Hayes, *The Biology and cultivation of edible mushrooms*, Acad. Press 1978). The species in question is *C. cinereus* (Schaeff. ex Fr.) S.F. Gray (according to Orton & Watling interfertile and thus conspecific with *C. macrorrhizus* (Pers. ex Fr.) Rea, and called *Coprinus fimetarius* by some authors). It is recommended because of the rapid development of the fruit bodies, but harvesting the small carpophores is extremely labor-intensive.

Another species of *Coprinus*, *C. radians* has proved to be responsible for the destruction of fabrics in the Pacific Islands. It must be assumed that this is only one of several species capable of inflicting damage to exposed clothing and equipment.

*C. quadrifidus* Pk. is said to produce an antibiotic called quadrifidin.

## SPECIES

Sect. 1. *COPRINUS* [*Comati* Fr. (1838) em. Lange (1915); *Pelliculosi* (Fr. 1838 ut *tribus*) em Schröter 1889]. Young pileus covered with a tomentum or with scales or fibrils, the tomentum, scales or fibrils formed exclusively by hyphal filaments, or else the pileus is without any macroscopical covering layer, and then the epicutis not cellular.

Type species: *C. comatus* (Müller in *Fl. Dan.* ex Fr.) S.F. Gray.

\*The *Pelliculosi* of Fries are termed a *tribus*, and correspond to what is otherwise considered as a subgenus. The next lower unit - to which the *Comati* belong - is therefore the section, as understood by Fries and the modern taxonomists.

Subsect. *Coprinus* (Annulati Lange 1915). Stipe with a distinct narrow annulus which is usually free or occasionally attached to the base of the stipe or with a cup-shaped volva; spores large, more rarely medium sized (10-25 µm in length); carpophores growing directly on dung or on manured ground, in ruderal places in gardens and parks, or lawns, on the ground in the woods, meadows, and alpine semideserts.

Type species: Same as in the section.

*C. comatus* (Müller in Flora Dan. ex Fr.) S.F. Gray; *C. sterquilinus* (Fr.) Fr.; *C. deserticola* Speg.; apparently also *C. vosoustii* Pilát.

Subsect. *Atramentarii* (Fr. 1838 ut sect.) Konr. & Maubl. 1924-37. Veil indistinct, on stipe not distinctively annulate and never free; spores usually smaller than 12 µm, sometimes with distinct ornamentation; growing near trees.

Type species: *C. atramentarius* (Bull. ex Fr.) Fr.

*C. atramentarius* (Bull. ex Fr.) Fr.; *C. insignis* Peck; obviously also *C. romagnesianus* Sing. [*C. atramentarius* var. *squamulosus* Bres.; *C. squamosus* (Bres.) Romagnesi, non Morgan] and *C. africanus* Pegler.

Subsect. *Alachuanii* Sing. (1949) (sect. *Picacei* Fr. 1838; *Impexi* Romagnesi in Kühn. & Romagnesi 1953). Cuticle of the pileus made up by filamentous hyphae with small side-branches and branchlets, often branching off at an approximately right angle and forming a dichophysoid structure usually colored tawny, sometimes thick-walled.

Type species: *C. alachuanus* Murr.

*C. alachuanus* Murr.; *C. herbivorus* Sing. obviously also 13 European species close to *C. alachuanus*, such as *C. utrifer* Joss.; *C. friesii* Quél.; *C. picaceus* (Bull. ex Fr.) S.F. Gray; *C. urticaecola* (Berk. & Br.) Buller (*C. brassicae* Peck); *C. gonophyllus* Quél. and obviously *C. clastophyllus* Maniotis; probably also *C. extlectorius* (Bull. ex St-Amans) Fr. (vix *A. extlectorius* sensu St-Amans according to Orton & Watling).

Note: A group with non-smooth spores may be temporarily attached here, e.g. *C. echinosporus* Buller (but may eventually represent a subsection of its own).

Subsect. *Lanatuli* (Fr.) Sing. (sect. *Lanatuli* Fr., Epicr. p. 250. 1838). Surface patches of the pileus made up of a trichodermium of simple, large, hyphal cells.

Type species: *C. lagopus* (Fr.) Fr.

*C. lagopus* (Fr.) Fr.; *C. lagopides* Karst.; *C. fimetarius* (L. ex) Fr.; *C. cinereus* (Schaeff. ex Fr.) Fr.; *C. radiatus* (Bolt. ex Fr.) Fr.; *C. pseudoradiatus* Kühner & Joss.

Note: Some characteristic sand-dune and desert fungi like *C. psamathonophilus* Speg. may be temporarily attached to this subsection unless, combined with *C. arenarius* Pat., they require an additional subsection.

Sect. 2. *MICACEI* Fr. (1838) em. Schröter in Cohn (1889) (*Furfurelli* Fr. 1838 p.p.; *Farinosi* Lange subsect. *Micacei* 1915). Cuticle or veil made up partly or entirely of

spherocysts or at least chains of isodiametric elements; annulus and volva absent but surface of pileus not naked nor covered by (microscopical) hairs or setae; carpophores mostly medium to large, not floccose-woolly from a veil.

Subsect. *Domestici* Sing. (1948). Covering layer of the pileus formed not exclusively of spherocysts and isodiametric elements, but the latter intermixed with a large number of fibrils and filaments.

*C. domesticus* (Bolt. ex Fr.) S.F. Gray (sensu Lange); *C. radians* (Desm.) Fr. and many other species (cf. Romagnesi, *Rev. Myc.* 10: 88. 1945) in Europe and North America; in South America: *C. carbonicola* Sing.; *C. uspallatae* Sing.; *C. sclerobasidium* Sing.; *C. hylaeae* Sing.

Subsect. *Exannulati* Lange (1915). Veil composed of spherocysts exclusively or with thin-filamentous connective hyphae intermixed.

Type species: *C. micaceus* (Bull. ex Fr.) Fr.

*C. micaceus* (Bull. ex Fr.) Fr.; *C. saccharinus* Romagnesi (ined.); also several other species.

Sect. 3. *CYCLODEI* Fr. (1838) (*Vestii* (Lange) Kühner & Romagnesi) Pileus without small erect unicellular hairs; partial veil often abundant, making the margin of the pileus or the stipe floccose-woolly; annulus or volva often present, or spores with strongly developed perisporial bag (KOH).

Type species: *C. hendersonii* (Berk.) Fr.

*C. niveus* (Pers. ex Fr.) Fr.

*C. niveus* (Pers. ex Fr.) Fr.; *C. stercorarius* (Bull. ex St-Amans) Fr.; *C. ebulbosus* Peck; *C. bulbillosus* Pat. (probably = *C. hendersonii* (Berk.) Fr. = *C. ephemeroides* (Bull. ex Fr.) Fr.; *C. patouillardii* (Quél.) Pat.; *C. martinii* Favre; *C. hypsizygus* Sing.; *C. saccosporus* Sing.; *C. narcoticus* (Batsch ex Fr.) Fr.

Sect. 4. *HEMEROBII* Fr. (1838). Pileus without any veil and epicutis of the pileus made up of a hymeniform layer of subisodiametric cells as in *Psathyrella*, or else pileus generally as well as the stipe covered by very small, (but mostly distinguishable under a lens or the dissecting microscope) unicellular, hyaline hairs. Mostly small, thin species which tend to dry up membranously in age, lamellae deliquescent or not.

Type species: *C. hemerobius* Fr. (in the sense of Lange = *C. auricomus*, subsect. *Auricomi* Sing., in the sense of Ricken = *C. plicatilis*, subsect. *Glabri* Lange).

Subsect. *Glabri* Lange (1915). Hairs and setae none.

*C. plicatilis* (Curt. ex Fr.) Fr. and obviously also *C. miser* Karst. sensu Lange.

Subsect. *Auricomi* Sing. (1948). Pileus with setae (erect colored thick-walled sparse and large hairs).

*C. auricomus* Pat.

Subsect. *Setulosi* Lange (1915). Pileus generally with small unicellular hyaline erect hairs visible under a good hand lens.

Type species: *C. disseminatus* (Pers. ex Fr.) S.F. Gray.

*C. disseminatus* (Pers. ex Fr.) S.F. Gray (*Agaricus*, Pers. ex Fr. 1821; *Coprinarius*, Kummer; *Pseudocoprinus*, Kühner); *C. angulatus* Peck (*C. boudieri* Quél.); *C. sub-impatiens* M. Lange & Smith; *C. subrenispermus* Sing.; *C. heterosetulosus* Locquin and many other species, cf. Kühner & Romagnesi (1953, p. 377-381) and M. Lange (1952).

### Subfamily Psathyrelloideae (Kühner) ex Singer

*Lilloa* 22: 461. 1951 ex *Sydotwia* 15: 67. 1961.

Type genus: *Psathyrella* (Fr.) Quél.

Syn.: *Psathyrellés* Kühner, *Bull. Soc. Myc. Fr.* 52: 33. 1936.

*Scotospores* Romagnesi, *Revue de Mycologie* 1(1): 33. 1936 (ut series, nom. nud.).

*Scotoporaceae* Romagnesi, *Rev. Myc.* 2(6): 245 (ut familia, nom. nud.). 1937, trib. *Psathyrelleae* Romagnesi, l.c.

*Scotoporoideae* Sing., *Ann. Mycol.* 34: 339. 1936 (ut subfamilia).

Characters: Lamellae wedge-shaped; spores discolored in  $H_2SO_4$ . Surface of pileus not radially grooved-splitting.

#### KEY TO THE GENERA

- A. Base of stipe with a well developed cup-shaped large membranous volva. 127. *Macrometula*, p. 111  
A. Volva indistinct or fugacious or none. 128. *Psathyrella*, p. 111

### 146. MACROMETRULA Donk & Sing., apud Singer

*Mycologia* 40: 264, 1948.

Type species: *Agaricus (Chitonia) rubriceps* Mass.

Characters: Habit of the carpophores somewhat like that of a *Volvariella* (pluteoid but volvate), with the lamellae not quite free but adnexed as in *Psathyrella*; pileus with a distinct cellular epicutis as usual in *Psathyrella*, the isodiametric elements densely packed, somewhat smaller in the lower layer and there somewhat brownish in KOH; basidia of the normal size as found in *Psathyrella*, 4-spored; cystidia ventricose below and somewhat narrowed or capitate above; also occasional echinulate bodies seen; spores small, with broad and flattened germ pore, light umber in KOH, strongly discolored by  $H_2SO_4$ , with smooth complex wall, the endosporium (which is hyaline) and the episporium about equally thick; trama of the lamellae sub-regular, consisting of light brownish, subparallel hyphae when revived in KOH; neither the trama nor any part of the spore wall pseudoamyloid or amyloid; subhymenium very dense, of small elements; stipe central, hollow, exannulate but with

a strongly developed cup-shaped membranous volva at the base with the free limb not attached to the surface of the stipe; context white, consisting of hyphae with clamp connections. On soil in greenhouses.

*Development of the carpophores:* Obviously "hemiangiocarpous"; not known in detail.

*Area:* The distribution of this genus is obscure since the only species known occurs in the Aroid house in Kew, England, and had obviously been introduced to Europe with some aroids.

*Limits:* This genus is clearly distinct from *Psathyrella* which never has a well developed volva. The presence of a volva is in other cases considered as a generic character (*Amanita*, *Volvariella*, *Clarkeinda*), and there is no reason why it should not be the main differentiating character in this case; at least under the presumption that no intermediates exist, the hiatus between the two genera is sufficiently large.

*State of knowledge:* A small fragment of the edge of the lamellae which was taken from the type specimen at Kew was studied by Donk and Singer at the Farlow Herbarium; later, more material was made available by the Director of the Kew Gardens, also from the type collection, clearly showing the presence of cystidia on the sides of the lamellae and the structure of the cuticle. This historical material in addition to the good picture published by Cooke, and Massee's original description, provide enough data on this fungus to insert it in the list of valid genera in the Coprinaceae.

*Practical importance:* None.

## SPECIES

*M. rubriceps* (Mass.) Donk & Sing. (*Agaricus*, Mass.; *Chitonia*, Mass.).

### 147. PSATHYRELLA (Fr.) Quél.

*Champ. Jura Vosg.* p. 178, 1872-3.

*Type species:* *P. gracilis* (Fr.) Quél.\*

*Syn.:* *Agaricus* subgenus *Psathyrella* Fr., *Epicrisis* p. 237. 1838.

*Psathyra* Kummer, Führ. Pilzk. p. 20. 1871 non Spreng. (1818).

*Psathyra* (Fr.) Quél., *Champ. Jura Vosg.* p. 148, 1872-3.

*Hypholoma* (Fr.) Quél., l.c. p. 112 (also sensu Romagnesi (1936), vix Kummer 1871\*\*).

\*The protologue (*Epicrisis* p. 237, 1838) would make *A. disseminatus* a rather marginal species, not best agreeing with the diagnosis and therefore rejected as lectotype. *A. disseminatus* has later been selected as type of a split genus, *Pseudocoprinus* by Kühner. Its independence from *Coprinus* is not yet generally rejected (see also p. 518).

\*\*The typification of *Hypholoma* (Fr.) Quél. and *Hypholoma* Kummer has been commented on by Donk, Singer, Dennis, Wakefield & Bisby, and the result of these nomenclatorial notes has been complete confusion. While Romagnesi (1936) thought of *Hypholoma* as constituent part of *Psathyrella* (*Drosophila*), other

*Pannucia* Karst., *Bidr. Finl. Nat. Folk* 32: xxvi. 1879.

*Drosophila* Quél., *Enchiridion* p. 115. 1886.

*Drosophila* Quél. subgen. *Hypholoma*, l.c.

*Lacrimaria* Pat., *Hymenom. Europ.* p. 122. 1887.

*Astylospora* Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 376. 1889.

*Glyptospora* Fayod, l.c. p. 377.

*Pluteopsis* Fayod, l.c. p. 377 (see also p. 540!).

*Cortiniopsis* Schröter in Cohn, *Cryptog.-fl. Schles.*, *Pilze* p. 566. 1889.

*Gymnochilus* Clements, *Bot. Surv. Nebr.* 4: 23. 1896, non Blume.

*Hypholomopsis* Earle, *Bull. N. Y. Bot. Gard.* 5: 436. 1909.

**Characters:** Pileus campanulate, conical or vesiculose at first, frequently or mostly distinctly hygrophanous often glittery when faded, with a distinct cellular to hymeniform epicutis, but rarely a true epithelium formed, more rarely the epicutis covered by a fibrillose velar layer and exceptionally (in this latter case) the epicutis proper suppressed; lamellae narrowly adnexed (rarely subfree) to adnate, more rarely adnato-subdecurrent; hymenophoral trama regular (in primordia divergent, in age subregular), pigmented or hyaline; basidia normal (comparatively somewhat larger than in *Agaricus*, sometimes 2-spored, without siderophilous granulation); pseudoparaphyses not regularly interrupting the basidia in the hymenium and generally not bi- or trimorphic; cross-section of the lamellae conical (lamellae wedge shaped), hymenophore not deliquescent; spore print purplish fuscous, cinnamon-fuscous, deep fuscous ("Rembrandt", "Java br." to "Hindu", "Cochin" to "Mandalay", M. & P.) to black, more rarely a dull reddish or russet e.gr. "deep brownish vinaceous" (Ridgway), transparent or opaque, with a usually truncate germ pore, rarely with non-truncate very narrow germ pore and in few species without a trace of a germ pore, smooth (rarely extremely finely punctate) and with homogeneous wall, but in section 1 verrucose or verruculose, sometimes with a

authors wished to typify the genus so that either a *Psathyrella* or a *Naematoloma* became the generic type of *Hypholoma*; consequently both generic names - *Psathyrella* and *Naematoloma* - have at times been replaced by *Hypholoma*. Since both *Psathyrella* and *Naematoloma* have been widely accepted by modern taxonomists, three different sets of names for large, important genera have been in use competing with *Psathyrella* and *Naematoloma*, simply because the authors interested in nomenclature could not agree on the type species for *Hypholoma*. In order to solve the problem satisfactorily, we have to keep in mind that (1) the type selection must be made from the species in Kummer 1871 insofar as they are also represented in Fries (if "(Fr.) Kummer" is cited), or independently of Fries (if "Kummer" is cited - the citation preferred by the present author); but in both cases the outcome would be the same; (2) that the revival of a generic name which has been interpreted by taxonomists in the history of agaricology in several quite different ways is not desirable and should be supported only if unavoidable.

Singer (1951) was the first to propose a type based on Kummer's genus. Since *H. velutinum*, the type, is in contradiction with the generic description (derived from all key characters) - as, by the way, are also the descriptions of the other species enumerated and described by Kummer - Kummer's genus becomes, together with its type species, a nomen dubium. If, as Donk and his followers want it, *Hypholoma* Kummer is accepted as a new status rather than a new genus, the first choice of a type species of the name based on *Agaricus* tribus *Hypholoma* Fr. 1821 would be Parker's (*Mycologia* 25: 169. 1933): *H. lachrymabundum* ... em. Quél. which refers to *Lacrimaria* and is apparently the same as my choice for *Hypholoma* Kummer, viz. *H. velutinum* (*H. lachrymabundum* sensu Quél. is not represented as such in Kummer and could not possibly be). If it is thought that Parker's specification "sensu Quélét" is applicable to Kummer's description in spite of the contradictions in Kummer's descriptive data, *Psathyrella* and *Hypholoma* would be based on different but congeneric species. Since *Hypholoma* would have the priority, *Psathyrella* would have to be proposed for conservation.

slightly rhomboid or subangular-tetrahedric (in frontal view) outline, small (rarely below 6  $\mu\text{m}$ ) to large (rarely above 20  $\mu\text{m}$ ), with complex wall, fading appreciably in concentrated H<sub>2</sub>SO<sub>4</sub>; veil present or absent, volva none; stipe central, usually tubulose, flexuous or straight; radicant or not, short white rhizomorphs sometimes present; context white or colored, mostly fragile-fleshy but often very thin in the pileus; hyphae usually with clamp connections, inamyloid. On the earth in- and outside the woods, often among mosses, on charcoal or ashes, on dung, straw and sand, even on living plants or on other agarics parasitically, and on various débris.

*Development of the carpophores:* "Hemiangiocarpous". According to Reijnders mostly bivelangiocarpous, more rarely almost monovelangiocarpous (*P. spadicea*) or paravelangiocarpous (*P. subatrata*) or metavelangiocarpous (*P. velutina*); hymenopileocarpic, hymenocarpic or isocarpic, more rarely (subg. *Lacrimaria*) pileocarpic or pileostipitocarpic. See also Hugueney (1965) for *P. coprobia* and Watling (1985) for subgen. *Lacrimaria*.

*Area:* Almost cosmopolitan.

*Limits:* Where, as in the majority of the species, the spore color is not rusty, the hymeniform or epithelial epicutis well developed and the spores with a distinct germ pore, the distinction of representatives of this genus presents no problems. Even if the hymenophore of some Coprini does not deliquesce, this happens in groups easily distinguishable from *Psathyrella* by the grooved-pectinate pileus and the anatomy of the surface layers, the development of the hymenium; and the finally flattened-parasol-like thin pileus. It is usually not difficult to distinguish *Coprinus* from *Psathyrella* in the field. Likewise, *Panaeolus* and *Panaeolina* as well as *Copelandia* and *Annellaria* are easily distinguishable macroscopically and the resistance of the spore pigment against concentrated sulphuric acid is a constant character separating the Panaeoloideae. By the same means one may distinguish dark-spored Agaricaceae and Strophariaceae, even in those exceptional cases where a *Psathyrella* does not show a distinct epicutis or germ pore (never both wanting in the same species!). There are two species of *Agrocybe* with particular-dark spore print, but here the spores have a more ochraceous color under the microscope than is usual in *Psathyrella*, and this color is persistent in H<sub>2</sub>SO<sub>4</sub>.

*Lacrimaria* Pat. has been admitted as a genus by all authors mentioned above, but after a discussion of the matter between the North American specialist of this genus, A.H. Smith, and the author, and after further comparison of representative specimens, the genus *Lacrimaria* does not appear to be well founded. The roughness of the outer spore wall has several times been found to be a character of specific rather than generic value. Otherwise, the species of *Lacrimaria* are not clearly separable from the species of that part of *Psathyrella* called *Hypholoma* sensu str. (not section) by Romagnesi (non al.). Since the name *Hypholoma* has been preoccupied by Romagnesi himself for a section different from the *Lacrimaria* group, *Lacrimaria* plus *Hypholoma* Romagnesi have been reunited here under the subgeneric name *Lacrimaria*. This emended concept of *Lacrimaria* is still not an autonomous genus. The author agrees with Kühner (1936) who stated his belief in the generic identity of *Hypholoma* sensu str. Romagnesi and *Psathyrella*.

Reijnders (1952) thought that *Lacrimaria* differs in its development pattern from the rest of the genus *Psathyrella*. However, in the table published by him in 1963 where more species are represented, the differences do not appear sharp enough to justify generic separation of *Lacrimaria* on that account, at least as long as it still appears that section *Psathyroides* is intermediate in carpophore development as well as in other regards. As in *Coprinus*, there is obviously a great amplitude of variation in development patterns also in other genera of the Coprinaceae. These observations will eventually become important in the definition of the sections and subgenera in both these genera. (see also Reijnders in Persoonia 10: 383-424. 1979).

*State of knowledge:* *Psathyrella* was a neglected genus from the taxonomic point of view, and there still is no world monograph in spite of the significant progress seen in Romagnesi's Kühner & Romagnesi's, A.H. Smith's and other contributions to the *Psathyrella* taxonomy in Europe and North America\* and the detailed studies on tropical and Patagonian species by the present author. Nevertheless, enough is known now in order to present a taxonomic outline of the infrageneric taxonomy of *Psathyrella* with sufficient examples of well known species. 74 species are here recognized.

*Practical importance:* *P. candelleana* is an excellent edible fungus but little used and better known in North America (as *Hypholoma incertum*) than in other regions. Some species are parasitic but apparently without major importance as pathogens of cultivated plants.

Drosophilin is an antibiotic substance obtained by Kavanagh et al. (*Antibiotic substances from Basidiomycetes IX, Proc. Nat. Acad. Sc. USA* 37: 570-574, 1952) from carpophores of *P. subatrata*.

## SPECIES

Subgenus I. ***Lacrimaria* (Pat.) Sing. & Smith in Sing. (1951) (*Drosophila* subg. *Pluteopsis* (Fayod?\*\*) Kühner & Romagnesi 1953; subgen. *Pseudostropharia* A.H. Smith). A fibrillose innate or superficial mostly tan-colored (mostly pigmented) layer forms the continuation of the veil on the surface of the pileus, partly covering or at times almost suppressing the epicuticular layer; spores sometimes verrucose or verruculose; pileus usually rather large (over 20 mm broad); stipe often relatively short or fleshy; veil sometimes annular; if the fibrils of the pileus are not distinctly pigmented and the spores smooth, but then the base of the stipe either with**

\*See especially A.H. Smith, The North American species of *Psathyrella*, *Mem. N.Y. Bot. Gard.* 24: 1633. 1972. - On European *Psathyrella* many new data will be found in E. Kitts van Waveren, Notes on the genus *Psathyrella* I-VII, *Persoonia* 6-11. Many additional species are described in these papers, as well as in recent papers by Romagnesi (*Bull. Soc. Myc. Fr.* 91: 137-224, 1975; 92: 189-206, 1976; 98: 5-68, 1982). Since the majority of these species have not been restudied by the present author (and since the species concept in *Psathyrella* does not seem to be satisfactorily settled), there is no need to add them to our enumeration. For an attempt at specific identification, the papers are, however, of great importance. The literature on tropical and Eastern species (Dennis, Pegler, Singer, Guzmán, Hongo) is even more scattered.

\*\*See p. 540.

squarrose scales or yellow (or both), and cystidia or metuloids often with amyloid contents and pseudomembrana, not however with greening exudate in ammonia nor with apical finger-like appendages and brownish wall, nor with abundant crystalline incrustations.

Type species: *P. velutina* (Pers. ex Fr.) Sing.

Sect. 1. *LACRIMARIA* (Pat.) Spores verrucose to verruculose, usually very dark even under the microscope and spotting the lamellae at maturity.

Type species: *P. velutina* (Pers. ex Fr.) Sing.

*P. velutina* (Pers. ex Fr.) Sing.; *P. sepulchrorum* Sing., Smith & Guzmán; *P. valdiviana* Sing.; *P. glareosa* (Favre) Moser in Gams; *P. polytricha* (Holmsk. ex Fr.) Moser in Gams. Several other species belong here according to A.H. Smith.

Sect. 2. *PSATHYROIDES* (Lange) Sing. (subgen. *Pluteopsis* (Fayod?) Kühn. & Romagnesi, Lange as section of *Hypholoma*, K. & R. as subgenus of *Drosophila*). Spores smooth, strongly to weakly pigmented.

Type species: *Hypholoma melanthinum* (Fr.) Karst. (sensu Lange) (= *P. maculata* (Parker) Moser in Gams).

*P. weberi* (Murr.) Sing.; *P. scabinacea* (Fr.) Konr. & Maubl.; *P. maculata* (Parker) Moser in Gams; *P. caputmedusae* (Fr.) Konr. & Maubl. (sensu Ricken, Bres. \*); *P. metuloidophora* Sing.; *P. squarrosiceps* Sing.; *P. battarae* (Fr.) Konr. & Maubl.

Subgenus II. **Homophron** (Britz.) Sing. (*Agaricus* subgen. *Homophron* Britz., *Ber. Naturh. Ver. Augsb.* 27: 174. 1883). Not combining the characters of the preceding subgenus; cystidia on the sides of the lamellae ventricose-ampullaceous or ventricose-conical, metuloid, thick-walled at least near apex rarely rather thin-walled throughout, strongly, more rarely slightly muricate with incrusting crystals and often somewhat colored, not with amyloid contents or green exudations in ammonia mounts; margin of pileus often involute; veil none or present and then white or pallid; pileus often relatively fleshy and rather thick (but small and thin in sect. 2); stipe often fasciculate on trunks, but also on other habitats; spore print in some species tending to "deep brownish vinaceous" (dull reddish).

Type species: *P. spadicea* (Schaeff. ex Fr.) Sing.

Sect. 1. *CYSTIDIOSAE* A.H. Smith (1972). At least many cystidia metuloid (thick-walled at least towards apex).

Type species: *P. cystidiosa* (Peck) A.H. Smith.

*P. olympiana* A.H. Smith; *P. sарcocephala* (Fr.) Sing. sensu Fr. non al.; *P. cystidiosa* (Peck) A.H. Smith (unless too close to the preceding species); *P.*

\*Since the cystidia of this species are not fascicled in bunches of two to four, Alexander H. Smith (l.c.) separates *P. caputmedusae* and related species from subgenus *Lacrimaria* making it the central species of a new subgenus: *Pseudostropharia* A.H. Smith. As long as a clearer separation between this and subgenus *Mycophila* (Smith's *Candolleana*) cannot be elaborated, I prefer to follow Kühner & Romagnesi who insert *P. caputmedusae* in their subgenus *Pluteopsis* sect. *Psathyroides*.

*amstelodamensis* Kits Van Waveren (unless too close to *P. sardocephala*); *P. muricellata* Sing.; *P. crinipellis* Sing.; *P. macquariensis* Sing.; *P. spadicea* (Schaeff. ex Fr.) Sing.; *P. subcernua* (Schulzer) Sing. (*Clitopilus conissans* Peck; *Psilocybe*, Peck\*).

Sect. 2. (unnamed\*\*). Cystidia thin-walled, but strongly apically incrusted; in contrast to sect. 1, where most species are relatively fleshy, the proposed type and only species has the habit of *Coprinus disseminatus* as aptly stated by Kühner & Romagnesi (1953).

*P. pygmaea* (Bull. ex Fr.) Sing. sensu Kühner & Romagnesi, probably also sensu Bulliard and Fries.

Subgenus III. **Mycophila** A.H. Smith (1973) (*Drosophila* sect. *Candolleanae* Romagnesi\*\*\*; subg. *Candolleana* A.H. Smith 1973) Pleurocystidia present or absent, if present - utriform and undivided and not exuding drops which turn green in NH<sub>4</sub>OH, if absent cheilocystidia mostly utriform or at least slightly narrowed in the middle with a neck generally not narrower than half the diameter of the ventricose part beneath or vesiculose; veil appendiculate or absent; not combining the characters of the two preceding subgenera.

Type species: *P. epimyces* (Peck) A.H. Smith

Sect. 1. **FRAGILISSIMAE** (Romagnesi 1944) Sing. (1951). Trama of the lamellae hyaline, entire trama very little pigmented (if at all), but at least the larger portion of it completely hyaline; cystidia on the sides of the lamellae none; spores larger than 10 µm.

Type species: *P. marcescibilis* (Britz.) Sing.

*P. marcescibilis* (Britz.) Sing. (*Psathyra fragilissima* Lange); *P. involuta* (Romagnesi) Moser in Gams.

Sect. 2. **CANDOLLEANAE** (Romagnesi) Sing. (*Candolleanae* Romagnesi as section *Drosophila*). Trama of the lamellae hyaline; cystidia on the sides of the lamellae none or very rare; spores smaller than 10 µm. (Tramate lamellarum hyalino; cystidiis ad latera lamellarum nullis vel rarissimis; sporis minoribus quam 10 µm).

\*Schulzer's spore measurements are very frequently incorrect. The European form has elongated spores, also according to Moser and Maire and does not differ in any important characters from the American species.

\*\*The appropriate sectional name should not be proposed before the nomenclatorial status of *P. pygmaea* (Bull. ex Fr.) Sing. sensu Kühner & Romagnesi (and probably Quélet) is cleared up. Pegler (1977) describes the cystidia as with thickened wall and metuloid which refers his species - although small and translucent striate - to sect. 1. He, like Moser, indicates *Psathyrella consimilis* and *Hypholoma minutellum* as synonyms but at least the latter (type WU) has floccose veil on the pileus and thin-walled cystidia without crystalline incrustation; the spores have no germ pore.

\*\*\*The type species of *Drosophila* is undoubtedly (Art. 8.1, Intern. Code) *D. candolleana*. The same type species corresponds to subgenus (section?) *Hypholoma* "Q." which, however, we do not use for subgenus III because it (1) is erroneously attributed to Quélet (see *Flore Mycologique* p. 60), (2) if attributed to Fries cannot be used for a section of subgenus III in *Psathyrella*.

*Type species: P. candolliana* (Fr.) Maire in Maire & Werner.

*P. candolliana* (Fr.) Maire in Maire & Werner, with f. *candolliana*, f. *incerta* (Peck) Sing. and f. *coriaria* (Pan.) Sing. [*Hypholoma candelleanum*\* (Fr.) Quél.; *Drosophila*, Quél.; *Hypholoma coriarium* Panuzzi]; forms of *P. candolliana* are often referred to as *Hypholoma incertum* (Peck) Sacc. - a separate species according to A.H. Smith: *P. incerta* (Peck) A.H. Smith, or as *Hypholoma appendiculatum* aut. which, in the sense of Fries is a species of doubtful standing, probably = *P. hydrophila* (sect. *Hydrophilae*); also here *P. hymenocephala* (Peck) A.H. Smith and *P. leucotephra* (Berk. & Br.) Orton and a related tropical species with scattered pleurocystidia: *P. annulosa* Sing.

Sect. 3. *COPRINOCIPITES* Sing.\*\* differing from sect. 2 in the absence of a veil.

*Type species: P. coprinoceps* (Berk. & Curt.) Dennis sensu Dennis

*P. coprinoceps* (Berk. & Curt.) Dennis sensu Dennis; *P. albocapitata* Dennis; *P. lignatilis* Sing. ined.; *P. castaneidisca* (Murr.) A.H. Smith.

Sect. 4. *SPINTRIGERA* (Fr.) Konr. & Maubl. (1948). Young trama of the lamellae pigmented (dark brown, or at least the hyaline hyphae intermixed with melleous ones) by intraparietal pigment. Typically annulate. Otherwise like section 2.

*Type species: P. spintrigera* (Fr.) Konr. & Maubl.

*P. spintrigera* (Fr.) Konr. & Maubl.; apparently also *P. pervelata* Kits V. Waveren.

Sect. 5. *OBTUSATAE* (Fr.) Sing. (*Fatuae* Romagnesi 1944 as section of *Drosophila*). Trama of the lamellae hyaline; cystidia on the sides of the lamellae present; spores rather small (smaller than 11 µm); carpophores often rather large.

*Note:* This is a rather large section based on *A. obtusatus* which is evidently the type species of sect. *Obtusati* Fr., *Epicr.* 232, 1838; it may be subdivided into several subsections or split up into at least three sections. For the time being - as we know relatively few species - we leave the section intact.

*Type species: P. obtusata* (Fr.) A.H. Smith.

1. Small species with practically pore-less spores.

*P. minutella* (Höhn) Sing.\*\*\*.

2. Larger species, not parasitic on other fungi, not showing muricate cystidia:

*P. spadiceogrisea* (Schaeff. ex Fr.) Maire in Maire & Werner (*Psathyra*, Kummer; *Drosophila*, Quél.; *Psilocybe*, Boudier); *P. groegeri* Hirsch (*P. vernalis* (Lange) Moser in Gams); apparently also *P. casca* (Fr.) Sing. and *Drosophila reticulata* Romagnesi.

\*The original spelling which is that of Fries 1821, was *candollianus*, and this is the one we have to follow; later Fries himself started to spell *candelleanus* and so did his followers.

\*\*Sect. n. A sectione *Candolleanarum* differt absentia veli. Typus: *Psathyrella copriniceps* (Berk. & Curt.) Dennis sensu Dennis, *Kew Bull. Add. Ser. III. p. 466. 1970*, Dennis 66 (K).

\*\*\*C.n. (*Hypholoma minutellum* Höhn, *Sitz.-ber. K. Akad. Wiss. 116, Abt. I: 98. 1907*).

3. Species parasitic on fungi, particularly the larger *Coprin*i (subgenus *Mycophila* A.H. Smith).

*P. epimyces* (Peck) A.H. Smith.

Sect. 6. *TYPHICOLAE* (Romagnesi 1944) Sing. 1951 ex Sing. (1961). Hymenophoral trama colored with intraparietal pigment (KOH, dried material); spores typically larger than 10  $\mu\text{m}$ ; cystidia on the sides of the lamellae none; carpophores small or rather small; lamellae rather narrowly adnexed. Typically in subaquatic habitats, with fugacious, fibrillose veil.

Type species: *P. typhae* (Kalchbr.) Pearson & Dennis.

*P. typhae* (Kalchbr.) Pearson & Dennis, and probably several other species including *P. rhizophorae* Sing.; possibly *P. riparia* (with spores 7.3-8.2  $\times$  4.8-5.3  $\mu\text{m}$ ).

Sect. 7. *HYDROPHILAE* (Romagnesi 1944) Sing. 1951 ex Sing. (1961). Trama of the lamellae colored with a intraparietal pigment (especially in KOH, dried material); spores small (up to 6.5  $\mu\text{m}$  long); cystidia absent on the sides of the lamellae, or more rarely present on both edges and sides; carpophores rather large (i.e. of the size of those of *P. candoliana* or slightly smaller); spores under the microscope generally not very deeply colored.

Type species: *P. hydrophila* (Bull. ex Mérat) Maire in Maire & Werner.

*P. hydrophila* (Bull. ex Mérat) Maire in Maire & Werner (Hypholoma, Quél.; Psathyra, Bertrand; Psilocybe, Gillet; Drosophila, Quél.).

Sect. 8. *FRUSTULENTAE* (Romagnesi) Sing. (*Indermediae* Kühn. & Romagnesi 1953). Differing from sect. 7 in spores measuring from 6 to 11.5  $\mu\text{m}$  in length, and in the constant presence of numerous pleurocystidia (which vary from utriform to ampullaceous with broad neck or rather narrow but rounded tip), also often in smaller size and very fugacious or, if initially abundant, entirely arachnoid veil.

Type species: *P. frustulenta* (Fr.) A.H. Smith (sensu A.H. Smith).

*P. frustulenta* (Fr.) A.H. Smith (sensu A.H. Smith); *P. subalpina* Sing. (Drosophila gossypina (Bull. ex Fr.) Quél. sensu Favre non sensu Lange nec Fr.); apparently also *Psathyra panaeoloides* Maire, *Drosophila ocellata* Romagnesi (*Psathyra frustulenta* sensu Lange); *D. pseudocorrugis* Romagnesi, and *P. subandina* Sing. (but possibly subgenus *Psathyrella*?).

Sect. 9. *ARGILLOSPORAE* Sing. (1973). Differing from sections 1-8 by practically not having any germ pore at the apex of the spore. Pleurocystidia absent or very rare.

Type species: *P. argillospora* Rick ex Sing.

*P. argillospora* Rick ex Sing.; *P. singeri* A.H. Smith; *P. subconocyboides* Sing.; *P. aequatoriae* Sing.; probably also *Drosophila empyreumatica* (Berk.) Kühn. & Romagnesi.

**Subgenus IV. Heterocystis** Sing. (1973). Cystidia either utriform or fusoid to ampullaceous, often brownish, grayish or yellowish and more or less thick-walled, with an exudate which becomes greenish in ammonia, with an entire or divided apex, in the latter case with horn- or finger-like appendages; veil present or absent; spores of medium size:  $6.5-12.5 \times 4.2-7 \mu\text{m}$ .

*Type species: P. dactylocystis* Sing.

Sect. 1. **HETEROCYSTIS**, Sing. 1975 ex Sing. Cystidia mostly brownish, grayish, or pale ochraceous, appendiculate or acute, basically ampullaceous or fusoid (Cystidiis haud hyalinis, ampullaceis vel fusoideis).

*Type species: P. dactylocystis* Sing.

*P. dactylocystis* Sing.; *P. moseri* Sing.; *P. phaeocystidiata* Sing.; possibly here: *P. xanthocystis* Orton and *P. hesleri-affinis* Sing.

Sect. 2. **SILVESTRES** Sing. (1973). Cystidia hyaline with broad neck and rounded apex, entire.

*Type species: P. silvestris* (Gillet) Moser in Gams.

*P. silvestris* (Gillet) Moser in Gams; *P. lutensis* Romagnesi; apparently also *P. narcotica* Kitts Van Waveren and (although some pleurocystidia vaguely grayish) *P. fascicularis* Sing.

**Subgenus V. Psathyra** (Fr.) Sing. (*Pannucia* (Karst.) Romagnesi 1944).\* Cystidia never utriform but rather ampullaceous or fusiform, with the apical portion less than half as broad as the ventricose one, neither thick-walled nor muricate, rarely with very slightly and rather evenly thickened wall which is sometimes beset with some crystals but then the other characters not coinciding with those of subgenus II; no greening exudate appearing on the surface of the cystidia when studied in ammonia; spores small (up to  $10.3 \mu\text{m}$ ). Species not combining the characters of the preceding subgenera.

*Type species: P. fibrillosa* (Pers. ex Fr.) Maire in Maire & Werner.

Sect. 1. **FIBRILLOSAE** Romagn. (1982). Spores with germ pore. (Sporis poro munitis)

*Type species: P. fibrillosa* (Pers. ex Fr.) Maire in Maire & Werner.

*P. nolitangere* (Fr.) Pearson & Dennis; *P. pennata* (Fr.) Konrad & Maubl. (sensu Ricken); *P. canocephala* (Kauffm.) A.H. Smith; *P. gossypina* (Bull. ex Fr.) Konrad & Maubl.; *P. fibrillosa* (Pers. ex Fr.) Maire in Maire & Werner (sensu Ricken); *P. atrifolia* (Peck) A.H. Smith; *P. polycystidiosa* Sing.; *P. acutissima* Sing.; *P. tristis* Sing.; *P. fulvescens* (Romagnesi) A.H. Smith; *P. communis* A.H. Smith.

Sect. 2. **APORA** Sing. (1973). Spores without germ pore.

*Type and only known species: P. apora* Sing.

\*Romagnesi separates two sections within this rather homogeneous group. There is a question whether or not such a separation is justified, and much seems to indicate that the subgenus should rather remain undivided. I am adding, however, a section for the species without germ pore.

**Subgenus VI. Psathyrella.** Distinguishable from the preceding subgenus mainly by the large spores which are mostly practically black in print or at least fuliginous-fuscous, and the characteristically ventricose to subvesiculose basidia with usually very narrow pedicel (not normally clavate-ventricose-constricted nor clavate-elongate), often broader than 6-10.3  $\mu$ m.

*Type species:* *P. gracilis* (Fr.) Quél.

*P. gracilis* (Fr.) Quél.; *P. microrhiza* (Lasch) Konrad & Maubl.; *P. ammophila* (Dur. & Lév.) Orton; *P. marthae* Sing.; *P. tilcariensis* Sing.; *P. subprona* Sing.; *P. patagonica* Sing.; *P. prona* (Fr.) Gillet (sensu Ricken); *P. atomata* (Fr.) Quél. (sensu Bres.); *P. conopilus* (Fr.) Konrad & Maublanc\*; *P. nothomyrciae* Sing.; *P. subatrata* (Batsch ex Fr.) Gillet.

**Subgenus VII. Conocybella** A.H. Smith in litt. ex Sing. (1948). Much like subgenus *Mycophila* but the cheilocystidia of the Conocybe-type. i.e. broadly ventricose below with a small globose stalked capitellum at the apex; pleurocystidia none; spores small (up to 10  $\mu$ m); veil absent, but pileus and stipe with a fugacious pubescence from narrow hyphae.

*Type species:* *P. michiganensis* A.H. Smith.\*\*

*P. michiganensis* A.H. Smith.

**Subgenus VIII. Cystopsathyra** Sing. (1961). Much like subgenus *Mycophila* but the velar vestiment of pileus and stipe powdery-mealy, consisting of spherocysts - an epithelium, detersile. Cystidia present, rather numerous on edges and sides, vesiculose-elongate or ventricose, sometimes with a constriction underneath the apex but not capitate, always broadly rounded, not muricate, thin-walled.

*Type species:* *P. kellermanii* (Peck) Sing.

*P. kellermanii* (Peck) Sing. (Galera, Peck).

#### Subfamily Panaeoloideae Sing.

*Ann. Mycol.* 34: 339. 1936 ex Sing., *Sydotzia* 15: 68. 1961.

*Type genus:* *Panaeolus* (Fr.) Quél.

*Syn.:* *Panaeolae* Romagnesi, *Rev. Mycol.* 2: 23. 1937 (*nom. nud.*) (ut tribus *Scotosporacearum*).  
*Panaeolés* Kühner *Bull. Soc. Mycol. Fr.* 52: 33. 1936 (série).

**Characters:** Pileus with cellular epicutis; lamellae not deliquescent, becoming very unequally dusted with the spores when mature, and consequently rather spotty when

\*Often erroneously quoted as *P. conopilea* (Weinm. ex Fr.) but see *Syst. Myc.* 1: 504. 1821.

\*\*Watling (1975) transfers this species (as *C. "michiganense"*) to *Conocybe*. His arguments in favor of this decision are based on the changes in pigmentation of the spores since deposition of the type, and on further anatomical details. While it is still perfectly possible to assume that here we have a case of convergence - precise data on stipe covering and hymenophoral trama structure are still missing from the descriptions of most Psathyrellae - we find Watling's argument worthy of consideration, see also p. 545.

seen from the sides, but belonging to the aequihymeniferous type, so-called *Panaeolus* subtype (Buller); spores often lemon-shaped, not discolored when treated with concentrated H<sub>2</sub>SO<sub>4</sub>; habit characteristically campanulate and rarely expanding, more rarely semiglobose and not expanding.

**Note:** G.M. Oláh (*Mém. hors-série d. l. Rev. d. Mycol.* 10; 1969) treats the Panaeoloideae in an important monograph, stressing particularly the chemical and cultural characteristics of the species known to him. In contrast to our treatment he lumps all genera under the single generic name *Panaeolus*, and combines this genus, following Heim (1957), with the family Strophariaceae rather than the Coprinaceae. He justifies this position of *Panaeolus* sensu lato with a synoptic table from which he deducts by a quasi-numerical method that the Panaeoloideae have more characters in common with the Strophariaceae than with the Coprinaceae. However, this method is neither theoretically correct nor based on a sufficient number of characters nor are the characteristics of the groups compared by him always correctly interpreted. If a numerical method like that developed by Machol & Singer (1972) had been used, the result would have been different as a tentative computation showed. The spore print colors in Strophariaceae are with a few exceptions different from those of *Panaeolus*; the presence of psychotropic alkaloids in both Strophariaceae (*Psilocybe*) and Panaeoloideae is of little help since such alkaloids are also present in some species of Bolbitiaceae and Cortinariaceae. The reactions of the pigments of the spores are only considered in their negative aspect, viz. the non-solubility of the pigments as a whole disregarding the fact that the non-soluble pigments of other families are not necessarily identical or comparable with those of *Panaeolus*. And the autodeliquescence of the lamellae is neither common to all Coprinaceae (not even all Coprini) nor absent from all other families compared (and not compared). The table also disregards the fact that the only character of *Panaeolus* which definitely and sharply separates *Psathyrella* from *Panaeolus* is the non-solubility of the spore pigment(s) in *Panaeolus*. It furthermore disregards the fact that one of the main differential characters between families of dark-spored agarics is the structure of the epicutis, quite and constantly different in Panaeoloideae and Strophariaceae. See also Clémenton (1975) and Machol & Singer (1977).

#### KEY TO THE GENERA

- A. Cystidia absent on the sides of the lamellae.
  - B. Spore print deep purplish fuscous or deep fuscous; spores warty. 148. *Panaeolina*, p. 535
  - B. Spore print black; spores smooth. 149. *Panaeolus*, p. 536
- A. Cystidia present on the sides of the lamellae.
  - C. Cystidia of the metuloid type; colored, thick-walled, acute; habit of the carpophores exactly as in *Panaeolus*. Context bluing. Predominantly tropical genus. 150. *Copelandia*, p. 538
  - C. Cystidia similar to the chrysocystidia, with refringent enclosure which is, however, not distinctly yellow in ammonia, with hyaline, thin wall and with broadly rounded apex; context not bluing.
    - D. Habit of the carpophores different from that of the typical *Panaeoli*: more fleshy and thick, never hygrophanous; stipe when young generally solid and white; cuticle viscid. Cosmopolitan genus. 151. *Anellaria*, p. 539
    - D. Habit typical of *Panaeolus*; stipe strongly pigmented, stuffed, soon tubulose; cuticle generally not viscid, strongly pigmented. Temperate. (See "B")

*Publ. Junta Ciènc. Nat. Barcelona* 1933, p. 109. 1933.

*Type species:* *P. foenisecii* (Pers. ex Fr.) R. Maire.

*Syn.:* *Psilocybe* Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 377. 1889, non al.  
*Psalliotina* Velen., *Nov. Myc.* p. 155. 1939\*

*Characters:* Those of the subfamily; spores in print deep purplish fuscous to deep fuscous (between "London smoke" and "bark" M. & P., between "warm sepia" and "bone brown" Ridgway); spores under the microscope finely to strongly warty, sepia-fuscous but transparent or almost so; pseudocystidia none; pileus pigmented; young margin straight (or almost so).

*Development of the carpophores:* Paravelangiocarpous, almost gymnangiocarpous; probably hymenocarpous (Reijnders 1963).

*Area:* Almost cosmopolitan (but probably introduced in many regions with grass seed).

*Limits:* This genus differs from rough-spored species of either *Coprinus* or *Psathyrella* by being neither deliquescent nor having a conspicuous veil, from both by the insolubility of the spore wall pigment.

*Panaeolina* is very close to *Panaeolus* and might be combined with it, as some authors propose. However, the color of the spore print is off black (between "London smoke" and "bark" M. & P.) and the spores are ornamented, both characters distinguishing this genus from *Panaeolus*. Among the species of the latter genus it comes closest to the hygrophanous, veil-less species *P. fimicola* sensu Oláh, *P. acuminatus*, *P. rickenii*, *P. subalteatus*, *P. moellerianus*, *P. convexulus* etc. - all of which have smooth spores, black in print, at first incurved margin of the pileus. It is also remarkable that wherever the lamellae during their development pass through a brown stage in *Panaeolus*, some bluing or bluish carpophoroids (sclerotia) are present. A species with smooth but rhombic spores which are somewhat nodose, *Panaeolina rhombisperma* Hongo, reminds one of *Crucispora* Horak. A germ pore on the spores is neither mentioned nor figured by Hongo. This interesting species should be restudied.

*State of knowledge:* One species is known to this author.

*Practical importance:* Carpophores may be a source of serotonin, 5-hydroxytryptophane and 5-hydroxyindolacetic acid since these substances were demonstrated to occur in quantities higher than usual (Tyler & Smith 1963), serotonin in amounts of 0.024% (the highest concentration of serotonin in any vegetable source).

\*Type seen (PR); no true annulus present; spores typical of this genus, as previously stated by Horak (1968).

## SPECIES

*P. foenisecii* (Pers. ex Fr.) Maire (Psilocybe, Quél.; Panaeolus, Kühner); possibly also *Panaeolus castaneifolius* (Murr.) A.H. Smith.

### 149. PANAEOLUS (Fr.) Quél.

*Champ. Jura Vosg.* p. 151. 1872-3, nomen conservandum.

*Type species: Agaricus papilionaceus* Bull. ex Fr.

*Syn.: Coprinarius* Kummer, *Führ. Pilzk.* p. 20. 1871.

*Chalymmota* Karst., *Hattsv., Bidr. Finl. Nat. Folk* 32: xxvii. 1879.

*Characters:* Pileus campanulate, more rarely conical, usually pigmented, rarely without pigment at first, not or little expanding in age, often more or less hygrophanous, appendiculate with a white or whitish, eventually black stained veil, or naked, viscid or dry; epicutis cellular; lamellae strongly variegated because of the basidia maturing in patches ("Panaeolus-subtype"), ascendant at least in youth; cheilocystidia present; other kinds of cystidia absent; rarely with chrysocystidia, and then carpophore small, dark colored; spores lemon-shaped, rarely more evenly ellipsoid, smooth, black in mass and almost so (not transparent) under the microscope, opaque, rather large (larger than 10 µm in most species known), with distinct broad germ pore, with thick, complex wall; stipe usually strongly elongated in comparison with the diameter of the pileus, rather thin, usually at least partly pigmented, tubulose, central. Context not bluing, but sclerotia sometimes bluing. On the soil and on dung (Pl. 73,6-8).

*Development of the carpophores:* "Hemiangiocarpous", at least in most species; Reijnders defines it as paravelangiocarpous or (in one species) almost gymnangiocarpous. Hymenocarpous.

*Area:* Cosmopolitan or nearly so.

*Limits:* See under the related genera of this subfamily.

*State of knowledge:* An attractive and interesting contribution towards the knowledge of this genus (in the broadest sense) has been made by G.M. Oláh (1969). Even so, the identification of the species of *Panaeolus* is still difficult, and the number of species and sections is difficult to establish. My own extensive studies on this genus do not permit me to coordinate my species with those of Oláh, and in certain species including even the supposedly well known (*P. campanulatus*, *P. sphinctrinus*), basic data are at variance. Thus, in species where Oláh indicates simple septa in cultures (presumably of secondary mycelium), I found clamped septa in tissue cultures; where Oláh found psilocybin present, my specimens yielded none (compare also Tyler in Petersen, 1971, p. 60 where Tyler points out that "it appears that ... there will be a large number of chemical races involved and that these may change under cultural conditions and according to the part of the country in which the material is collected"). This means that either the presence or absence of psilocybin and

psilocin is not important in specific taxonomy, or else Oláh's species are somehow different from those of some other authors. Also, some other characters often used for the distinction of species, are difficult to establish since they are not constant or lend themselves to different interpretations. Thus, the species which I have identified as *P. fimiputris* (sensu Bres.) has distinct appendiculate veil which often appears on the stipe as a narrow ring-zone, both concolorous with the surface of the stipe-apex. A culture from the carpophore collected by me produced identical carpophores in vitro, but the veil in these was reduced to an extremely fugacious cortina not leaving any traces on the margin of the pileus or the apex of the stipe.

The 14 species here enumerated have been fairly well defined and identified with those found in the literature. Few types are preserved.

*Practical importance:* A specimen of *Panaeolus sphinctrinus*, so determined by Linder and confirmed by me (FH) was sent in from Mexico as one of the hallucinogenic mushrooms used by the Indians in Oaxaca. Nevertheless, later visits by Heim and myself showed that this fungus is not used by the Mazatecos, Zapotecos, Nahuas, etc. On the other hand, there can be no doubt but that some species of *Panaeolus*, particularly *P. subbalteatus* (see Singer & Smith in Singer, 1958) do contain psychotropic substances, and Oláh was able to demonstrate the presence of psilocybin in this and a number of other species of the genus. Some of these produce intoxications or poisoning.

## SPECIES

1. Hygrophanous species without veil and without chrysocystidia - usually drying with a dark outer belt, fading from the center outwards.

*P. subbalteatus* (Berk. & Br.) Sacc. (*P. venenosus* Murr.); *P. moellerianus* Sing.; *P. acuminatus* (Schaeff. ex Secr.) Quél. (sensu Lange, Hora); *P. rickenii* Hora; *P. fimbriola* (Fr.) Gillet (sensu Oláh); apparently also *P. fontinalis* A.H. Smith; *P. uliginosus* J. Schäffer; *P. olivaceus* Møller.

2. Hygrophanous species (not drying with a dark marginal belt), without veil, without cystidia (chrysocystidia).

*P. convexulus* Sing.: *P. guttulatus* Bres. (*Psilocybe aleuriata* Heim & Remy according to Kühner).

3. Slightly hygrophanous (only along the margin, not drying with a belt-like zone) or non-hygrophanous species with a fugacious cortinoid to floccose veil, without cystidia (chrysocystidia).

*P. retirugis* (Fr.) Quél. (sensu Ricken, Singer 1969, non al.); *P. fimiputris* (Bull. ex Fr.) Quél. (sensu Bres. non al.); *P. phalaenarum* (Fr.) Quél. (sensu Singer 1969, non Bres. nec Oláh); *P. papilionaceus* (Bull. ex Fr.) Quél. (sensu Konrad & Maubl., Ricken non Weinm.); *P. campanulatus* (L. ex Fr.) Quél. sensu Oláh.

4. Slightly hygrophanous or non-hygrophanous species without a trace of a veil, without pleurocystidia.

*P. sphinctrinus* (Fr.) Quél. with var. *minor* (Fr.) Sing.; *P. uliginicola* (Speg.) Sacc.

##### 5. Cystidiate species (with chrysocystidia):

*P. ater* (Lange) Hora; obviously also *P. obliquoporus* Bon.

**Note:** *Agaricus campanulatus* L. ex Fr. (1838) is the same as either *P. simiputris* (which has priority) or *P. phalaenarum*; it has also been taken up (and it is difficult to prove that this has been done wrongly) to designate *P. papilionaceus* (which has priority) or *P. sphinctrinus* (because the latter is incorrectly described by Fries as having a veil; probably the appendages on the crenulate projecting margin were interpreted as a veil by Fries) and several other species. I consider it desirable to abandon the epithet *campanulatus* as a nomen dubium unless authentic material is found which can be proved to agree with one of the four species mentioned above.

#### 150. COPELANDIA Bres.

*Hedwigia* 53: 51. 1913.

**Type species:** *Copelandia papilionacea* (Bull. ex Fr.) Bres. (sensu Bresadola non *Panaeolus papilionaceus* (Bull. ex Fr.) Quél.).

**Characters:** Pileus and stipe pigmented or scarcely pigmented, but tending to turn blue when wounded or touched and mycelial cultures turning blue; hymenophoral trama regular; hyphae with or without clamp connections; spores smooth; metuloids on the sides of the lamellae rather numerous, with thick walls and subacute narrowly mucronate or elongated subampullaceous apex which is sometimes solid, generally incrusted by crystals at the apex; spores lemon-shaped, smooth, with broad, distinct germ pore, opaque, black in print; on soil and on dung. Pl. 77, 1-5.

**Development of the carpophores:** Unknown, but probably as in *Panaeolus*, easily fruiting *in vitro*.

**Area:** Tropics and subtropics in both hemispheres, besides sometimes introduced in the temperate zones (e.g. France).

**Limits:** The genus *Copelandia* differs sharply from *Panaeolus* (1) in the bluing context (as in *Psilocybe* sect. *Caerulescentes*), (2) the characteristic metuloids, not otherwise found in the Panaeoloideae (but similar ones occurring in *Psathyrella*).

**State of knowledge:** I know six species. As for details see *Lloydia* 42: 469-474. 1979, with key. The illustrations given by Oláh (1969, plate 19) are not characteristic for the fresh fungus.

**Practical importance:** The genus is characterized by the presence of psilocybin and psilocin, and is hallucinogenic. (Singer, *Acad. Nac. Cienc. Bol.* 41: 38. 1959; Singer & Weeks, *Lloydia* 42: 469-474. 1979).

## SPECIES

*C. cyanescens* (Berk. & Br.) Sing. (*Panaeolus*, Sacc.; *Copelandia papilionacea* (Bull. ex Fr.) Bres. sensu Bres. non *Agaricus papilionaceus* sensu Fr.; *C. tropicalis* (Oláh) Sing. & Weeks and *C. cambodiensis* (Oláh) Sing. & Weeks; *C. chlorocystis* Sing. & Weeks; *C. westii* (Murr.) Sing.; *C. bispora* (Malençon & Bertault) Sing. & Weeks.

### 151. ANELLARIA Karst.

Hattsv., *Bidr. Finl. Nat. Folk* 32: xxvii. 1879; em.

*Type species: A. separata* (L. ex Fr.) Karst.

*Characters:* Pileus comparatively fleshy (much more so than in *Panaeolus*), with very little pigment (practically white in most specimens, or which a slight ochraceous hue on the disc), viscid, with wide sterile projecting margin, campanulate, slightly expanding but not flattening in age, with well developed epithelium; lamellae variegated as in *Panaeolus*; hymenophoral trama regular but its elements not all truly parallel and not equal in size, some of them rather short; basidia normally clavate, 4-spored; cheilocystidia versiform; cystidioles of the sides of the lamellae very voluminous, vesiculose, some strongly suggesting the chrysocystidia of the Strophariaceae but not distinctly yellow in ammonia and not distinctly bluing in cresyl blue, strictly hyaline; spore print black; spores under the microscope deep purplish fuscous to black, opaque, smooth, always very large, with complex wall and broad distinct germ pore, not discolored in  $\text{H}_2\text{SO}_4$ , ellipsoid to lemon-shaped; stipe with or without traces of a veil, part or all of it often found on the fringe of the margin, either solid, or annulate, or both, rather fleshy, practically not pigmented, central, rather long, sometimes viscid; context white and unchanging, fleshy, consisting of hyphae with clamp connections. On dung and on manured soil.

*Development of the carpophores:* Probably always "hemiangiocarpous", paravélangiocarpous in *A. semiovata*.

*Area:* Cosmopolitan, one species in North America north to Michigan, otherwise nearly pantropical and subtropical; the other more boreal and montane.

*Limits:* The practical absence of coloring matter, combined with the gelatinosity of certain surface layers of the carpophores, the fleshy pileus and stipe not containing psilocybin, and the young solid, often annulate stipe are enough characters to define this genus macroscopically, even if it were not characterized by a simple, and dependable microscopical feature, the pleurocystidia, which it shares only with one very dark colored species of *Panaeolus*.

*State of knowledge:* Two species are known and all necessary data about them are available.

*Practical importance:* Both species are edible.

## SPECIES

### A. Annulate species, boreal and montane.

*A. semiovata* (Sow. ex Fr.) Pearson & Dennis [Panaeolus, Lundell & Nannfeldt; Panaeolus separatus (L. ex Fr.) Quél.; Anellaria, Karst.].

### B. Exannulate species, warm temperate to tropical.

*A. sepulchralis* (Berk.) Sing. [Panaeolus, Sacc.; Panaeolus solidipes (Peck) Sacc.; Panaeolus teutonicus Bride & Métrod; Panaeolus phalaenarum (Fr.) Quél. sensu Kühner & Romagnesi, non Sing. & Digilio, nec Fr.; *P. semiovatus* f. *exannulata* Pearson; *Agaricus capnolepis* Kalchbr.; *P. antillarum* (Fr.) Dennis sensu Dennis, Pegler, Reid, vix Fr.].

## GENUS INCOMPLETELY KNOWN

*Pluteopsis* Fayod, *Ann. Sc. Nat., Bot.* VII. 91: 377. 1889. The genus is based on *Agaricus pellospermus* Bull. ex Secr. sensu Secr. *Myc. Suisse* 1: 388. 1833. Formally, thus, *Pluteopsis* has been synonymized with *Psathyrella* inasmuch as both Bulliard pl. 571, 1 and Secretan's descriptions are without any doubt *Psathyrellas*, probably near *P. corrugis*. However, Horak (1968) points out that on the basis of the spore shape as illustrated by Fayod, *A. pellospermus* sensu Fayod might be rather a *Coprinus* of sect. *Setulosi* (here subsection, p. 523). Fayod's (type?) material found by me at G has *Psathyrella*-type epicutis, utriform cystidia, smooth, brown spores, clamp connections, fuscous pileus with venose umbo, adnexed lamellae. The specimens came from "Gorge de l'Avançon sous les Posses sur Bex". The identification *Pluteopsis pellospermus* was later (by Fayod) changed to *A. murcidus* Fr. (as *Psilocybe*). These data, tend to indicate that *Pluteopsis* refers to a *Psathyrella* near *P. spadiceogrisea*, different from *Pluteopsis* sensu Kühner, Kühner & Romagnesi, rather than to a *Coprinus* inasmuch as a second species of *Pluteopsis* "*P. tricholepis* nob." (Fayod) ined. (G) is undoubtedly referable to *Psathyrella*.

## BOLBITIACEAE Sing.

*Pap. Mich. Acad. Sc., Arts, Lett.* 32: 147. 1946 (publ. 1948).

Type genus: *Bolbitius* Fr.

**Characters:** Hymenophore lamellate; epicutis always consisting of piriform (erect) or globose cells, and then the pileus usually hygrophanous and often glistening when dry; dermatocystidia differentiated from the elements of the epicutis, or not; cystidia present only on the edges (cheilocystidia), or also on the sides of the lamellae, but true chrysocystidia very rarely occurring and then extremely scattered, but pleurocystidia sometimes somewhat thick-walled, more often thin-walled, rarely metuloid; spore print a very rich deep but bright (orange-)rusty color, more rarely ochraceous (*Descolea*), or ferruginous-fuscous to tobacco brown (*Agrocybe*, some

*Bolbitius*) approaching the spore color of *Inocybe*, rarely a deep fuscous brown to blackish brown (*Agrocybe*), under the microscope melleous ochraceous or rusty (sometimes becoming much deeper rusty in KOH mounts), yellowish ochraceous or light brown, rarely ornamented (punctate, verruculose, verrucose), generally with a broad, truncate germ pore, but in some species of *Agrocybe* germ pore narrow and often weakly or not truncate, or rarely (*A. erebia*-group) entirely absent or else (*Descolea*) replaced by a hyaline snout-like conspicuous callus (which makes the spores look somewhat like *Rozites*-spores) normally binucleate and with a hilum of the open-pore type; basidia often comparatively broad, 1-2-3-4-spored (two-spored races common and sometimes a species consistently two-spored); stipe fleshy to fragile, central, often with dermatocystidia; clamp connections mostly present, more rarely absent (in some species of *Bolbitius* and *Pholiota*, rarely in *Agrocybe*); growing on the soil and on litter, fruits, seeds, straw, dung, in- and outside the woods and forests, sometimes on sand dunes or on charcoal, in greenhouses, gardens, fields, lawns etc.

*Limits:* Sometimes (especially in *Agrocybe*), the cellular structure of the epicutis is not hymeniform throughout, but a careful study of the epicutis - even where covered or distorted by a velar layer, or fragmentary - always shows it to be at least in places hymeniform and quite different from the structure of the epicutis in similar species of the Strophariaceae. There is no transition from *Agrocybe* to Strophariaceae. The species of *Agrocybe* without a distinct germ pore have a strictly hymeniform epicutis and pleurocystidia; it is not difficult to distinguish them from either *Simocybe* or *Pholiota* or *Phaeomarasmius*. Romagnesi (1962) thought that some Simocybes are so close to some Agrocybes that the two genera should be combined. This view was based on an allegedly intermediate species, *Naucoria laevigata*, but my study of the type of the latter showed that it is a perfectly typical representative of *Simocybe* (lectotype, G), with fascicles or stretches of subhymeniform ventricose-clavate elements (dermatocystidia) and the spores have the reniform shape and the completely continuous spore wall of the apex (no trace of a pore) of many Simocybes, no pleurocystidia, and habit not at all like *Agrocybe* but like *Simocybe centunculus*. The similarity in color (tending to olive) in *A. firma* is not constant, and in itself cannot be a reason for combining two genera which are otherwise not even related.

In one or two species of *Agrocybe* and possibly *Conocybe* the spore print is dark or dusky enough to make one think of the Coprinaceae, but *Psathyrella* is immediately excluded by the partially soluble pigment in  $H_2SO_4$  (but see *Psathyrella michiganensis*, p. 533 and p. 545) and *Panaeolina* differs in ornamented spores. The occasionally somewhat aberrant features of *Agrocybe* are not encountered at the same time in any given species of that genus, and the spore print color - less rusty than in *Conocybe*, *Galerella*, *Bolbitius*, and *Pholiota* - are not in themselves a sign of affinity with other groups of agarics since the lack of a rusty-ferruginous color in the spores is also observed in some species of *Bolbitius* and these species are otherwise fully characteristic for *Bolbitius* in every regard and inseparable from that genus.

Horak (1970) and Watling (1979) think that *Descolea* differs by spore characters too much from the Bolbitiaceae and is too similar to *Rozites* to keep in the Bolbitiaceae.

I think their published observations do not prove this. The features enumerated by Horak have induced me to insert *Descolea* at first sight in the Cortinariaceae, but in the *Rozites*-group of the Cortinariaceae species with hymeniform epicutis are absent; all species are ectotrophically mycorrhizal, whereas *Descolea* is often non-mycorrhizal and always shows a hymeniform epicutis. The spore ornamentation is the same as that found in two species of *Pholiota* and several species of *Conocybe*, and the lack of a germ pore is not altogether foreign to the Bolbitiaceae. Horak thinks that *P. verrucispora* is probably a *Descolea*. If this were so, one of the important arguments in favor of inserting *Descolea* in the Bolbitiaceae would disappear; however, *P. verrucispora* has all the characteristics of *Pholiota* including spore print color, spore shape and absence of a veil, and the species is closely related to the European *P. subnuda* which has likewise ornamented (marbled) spores. Both have a rounded-obtuse spore-apex with a distinct germ pore, and no mucro.

*Galeropsis* is, as I have pointed out as early as 1936, a Gastromycete. It has the spores as well as the habit similar to such species as *Conocybe cylindracea* but the epicutis is not truly hymeniform and the basidia are not autobasidia so that no spore print is shed. Much more closely related to the Bolbitiaceae is another Gastromycete, *Gastrocybe lateritia* Watling. I have studied authentic material and agree with Watling that this is a gasteromycetoid genus with apobasidia, unable to shed a spore print (see also Singer & Ponce de Léon, *Mycotaxon* 14: 82-90. 1982), and p. 844).

#### KEY TO THE GENERA

- A. Spore print rusty, brown-ferruginous, sometimes almost (orange-)ferruginous, rarely ochraceous.
  - B. Pileus viscid and plicate-sulcate as in some Coprini; stipe white or whitish, rarely pink, even near the base; trama of the lamellae normally regular; cheilocystidia not abruptly capitate; lamellae often slightly deliquescent in age and pseudoparaphyses usually numerous. 155. *Bolbitius*, p. 550
  - B. Fungi not combining these characters.
    - C. Trama of the lamellae, at least in the narrower lamellulae or in the edge-near third of the through-lamellae consisting of a very reduced mediostratum, the hymenopodia of both sides of it very strongly developed and almost touching each other (*Conocybe*-type); veil mostly (though not always) completely absent, never forming an annulus; pileus plicate or cheilocystidia with a stalked globulose capitulum (abruptly capitate).
      - D. Pileus plicate-sulcate as in some Coprini; cheilocystidia not capitate. 153. *Galerella*, p. 546
      - D. Pileus subsulcate, transparently striate or smooth when moist or dried, not plicate; cheilocystidia abruptly capitate by a stalked capitulum. 152. *Conocybe*, p. 543
    - C. Trama of the lamellae normally regular (mediostratum well developed, many of its elements rather voluminous); veil present or absent, sometimes with an annulus; pileus never plicate-sulcate; cheilocystidia rarely capitate.
      - F. Spores with or without exosporial ornamentation, without a snout-like callus or mucro, with a broad or narrow (at least in frontal view) mostly truncate germ pore; annulus present or absent; spore print usually more or less rusty. 154. *Pholiota*, p. 547
      - F. Spores with a protracted mucro-like callus, always ornamented, without a distinct germ pore; annulus or double veil present, or at least a strongly developed veil present; spore print ochraceous. 156. *Descolea*, p. 549
  - A. Spore print ferruginous-fuscous (with a weak rusty shine) or tobacco brown to argillaceous brown, rarely deep brown, almost blackish brown, never bright rusty or ochraceous.
    - G. Lamellae almost linear, narrow; context of the pileus very thin; margin plicate-sulcate (see "B" above: *Bolbitius*).
      - G. Lamellae moderately narrow to very broad; context of the pileus comparatively thick and fleshy; margin not sulcate-plicate. 157. *Agrocybe*, p. 552

*Prodrome, Ann. Sc. Nat., Bot.* VII. 91: 357. 1889, nomen conservandum.\*

*Type species: Galera tenera* (Schaeff. ex Fr.) Kummer.

*Syn.: Pseudoconocybe* Hongo, *Journ. Japan. Bot.* 42: 153. 1967.

**Characters:** Habitat of the carpophores mycenoid, rarely assuming tricholomatoid appearance and then, because of the color of the lamellae, strongly reminiscent of *Cortinarius*; pileus hygrophanous, glistening when dry, not noticeably gelatinized in its outer layer with piriform to subglobose cells forming the epicutis; dermatocystidia on the stipe often present, but none or abruptly capitate on the pileus; lamellae usually at first strongly ascendant, the pileus not radially plicate-sulcate along the back of the lamellae but often transparently striate to somewhat sulcate; veil none, or slight on the margin of the pileus, none on the stipe; spore print a deep, rich, beautiful rust color; spores smooth or faintly verruculose, verrucose in some tropical species, with germ pore deep rust color (rarely paler rusty-melleous) in ammonia, lemon-shaped, lentiform, or mostly ellipsoid, in the lentiform spores a hexagonal outline (benzene formula) in frontal view often very marked; basidia broad and short, otherwise variable, especially in the number of sterigmata, 2-spored races frequent; cystidia on the sides of the lamellae not present in any species but cheilocystidia always present, very characteristic, ventricose below, with a globose capitulum which is stalked abruptly (Pl. 21,1); pseudoparaphyses often very striking; hymenium sometimes containing a substance that crystallizes in ammoniacal medium forming long colorless needles; hymenophoral trama reduced to a very thin mediostratum consisting of a few filamentous hyphae which are flanked by the enormously developed hymenopodium consisting of voluminous elements, the hymenopodia of both sides of the mediostratum almost touching each other, the whole trama making almost the impression of being bilateral but the flanking layer not divergent, rather all hyphae more or less parallel with each other (Pl. 27,2); stipe usually straight and central, elongate and thin, rarely thick-fleshy, often villous or pubescent, pruinose, etc., from hairs or dermatocystidia (which are often shaped like those of the edge of the lamellae), white or colored, with or without a pseudorhiza, rarely somewhat marasmoid; all hyphae with clamp connections in the normal (heterothallic) forms. In and outside the woods, not rare in greenhouses, fields and gardens, on the bare soil, or among mosses and grasses, or on decayed wood, on charcoal, on anthills, on dung, etc. sometimes on sand dunes.

**Development of the carpophores:** paravelangiocarpous or gymnangiocarpous, and probably always hymenocarpous, according to Reijnders (1963).

**Area:** Almost cosmopolitan (not in the Antarctic).

**Limits:** *Conocybe* is closest to *Galerella* and *Pholiota*. It is usually possible to recognize a representative of *Conocybe* in the field. In the laboratory it differs from *Galerella* in capitate cheilocystidia and non-pectinate margin. Kitts van Waveren

\*The genus *Conocybe* is not in need of conservation and may just as well be taken off the list of nomina conservanda.

(*Persoonia* 6: 121. 1970) attempts to minimize the difference in tramal structure of *Conocybe* and *Pholiotina* by saying, in effect, that it is different, in some cases, only in the edge-near region and the "small lamellae" (citing Kühner who discovered the character), and by theorizing that the differences in structure are indeed differences of stages of development. Since Kits van Waveren has not, as the present author, checked on this character himself and judges it only on the basis of the literature, I must insist on my own observations on numerous species of both genera - observations which coincide in every detail with the observations by Kühner. The fact that the structure has to be observed in certain restricted areas of the hymenophore, cannot distract from its general usefulness. It is furthermore not exact to say that I based the difference of both genera exclusively on the "alleged" difference in the hymenophoral structure since there are obviously also differences in the cystidial and dermatocystidial characters even though there is, in *Pholiotina*, an exception where the cheilocystidia are capitate, but where the veil is much more developed than in all species of *Conocybe* (even if there are some species of *Conocybe* with a very weak veil as I have first noted in *C. subvelata*, Singer 1950). It is finally incorrect to state, as did Kits van Wavern, that a generic separation of *Pholiotina* from *Conocybe* has been adopted only by Singer and Moser. This separation was adopted by Singer 1936 (not 1949) and onwards, and has been followed by many authors. Watling (in his survey of the Bolbitiaceae) also used *Pholiotina* as a subgenus of *Conocybe*, but apparently because he favors a wider generic concept rather than because he disagrees with the observations by Kühner and Singer.

Watling (1975) transfers the subgenus *Conocybella* of *Psathyrella* and its type species to *Conocybe*, see under *Psathyrella* (p. 533) and below (note after section *Pilosellae*, p. 545). If his argumentation is accepted the delimitation of both the Coprinaceae and the Bolbitiaceae is affected and should be slightly modified on p. 541. However, for the present, this thus far exceptional case is merely mentioned here and final action postponed until more data on *Psathyrella* become available.

*Pseudoconocybe* is so close to *Conocybe*, sect. 1 and 3 that, in spite of the different spore shape, I follow Watling (1976) who consideres it a section of *Conocybe*.

*State of knowledge:* An excellent monograph of lasting importance has been published by Kühner (1935); many (including many tropical) species were later studied by Singer (various papers) and additional data are due to Watling (various papers, especially *British Fungus Flora* 3. 1982). The number of species admitted here is 54.

*Practical importance:* Unknown.

## SPECIES

**Subgenus I. *Conocybe*.** Spores smooth, larger than 6  $\mu\text{m}$ ; stipe fragile and rather soft, not appearing marasmioid in dried specimens.

*Type species:* *C. tenera* (Schaeff. ex Fr.) Fayod ex auct.

Sect. 1. *CONOCYBE*. Stipe entirely covered with cheilocystidium-like (capitate) dermatocystidia, few dermatocystidia (or none) without capitulum, and no long hyphous hyaline hairs present among the dermatocystidia. Spores and nodulose.

Type species: *C. tenera* (Schaeff. ex Fr.) Fayod ex auct.

*C. mesospora* Kühn. ex Sing.; *C. brunneola* (Kühner) Kühner & Watling; *C. rickeniana* Sing. ex Orton; *C. spiculoides* Kühn. ex Sing.; *C. affinis* Sing.; *C. macrocephala* Kühn. ex Sing.; *C. semiglobata* Kühn. ex Sing.; *C. tenera* (Schaeff. ex Fr.) Fayod ex auct. (sensu Kühner); *C. striatipes* (Speg.) Sing. (*C. leucopoda* Kühner); *C. antipoda* (Lasch) Kühn. (*Galerula floridana* Murr.); *C. tenerrima* Sing. with var. *monticola* Sing.; *C. mamorensis* Sing.; *C. proxima* Sing.; *C. xerophytica* Sing.; *C. aurea* (J. Schaeff.) Kühner & Romagnesi ex Hongo; apparently also *C. rabenhorstii* (Fr.) Sing.

Sect. 2. *NODULOSPORAE* Watling (1976). Differing from sect. *Mixtae* and *Conocybe* in nodulose (reminding one of *Inocybe*) spores; stipe covering as in sect. 3.

Type species: *Pseudoconocybe nodulospora* Hongo.

*C. nodulospora* (Hongo) Watling; *C. javanica* Sing. ined.

Sect. 3. *MIXTAE* (Kühner) Sing. Stipe with cheilocystidium-like (i.e. capitate) dermatocystidia and at the same time with non-capitate dermatocystidia and hyphous, long, hyaline hairs.

Type species: *Galera megalospora* J. Schaeff.

*C. cryptocystis* (Atk.) Sing. (*Galerula*, Atk.; *Galera megalospora* J. Schäffer; *C. subpubescens* Kühner ex Orton); *C. diemii* Sing.; *C. alba* Sing.; *C. mixta* Sing.; *C. reticularrugosa* Sing.; *C. ambigua* (Kühner ex) Sing.; *C. tetraspora* Sing.; *C. xylophilus* Sing.; *C. macrorhiza* (Speg.) Sing. (?*C. dunensis* T.J. Wallace apud Orton); *C. urticae* (Velen.) Sing.\*

Sect. 4. *PILOSELLAE* (Kühner) Sing. Stipe not entirely white, with numerous hair-like hyphal elements which make the stipe strongly pubescent when quite fresh, but cheilocystidium-like dermatocystidia with abruptly capitate apex on the surface of the stipe absent or extremely rare at the extreme apex of the stipe.

Type species: *C. pilosella* (Pers. ex Fr.) Kühner.

*C. pilosella* (Pers. ex Fr.) Kühner (sensu Atk., Kühner); *C. anthracophila* (Maire & Kühner) Sing.; *C. mazatecorum* Sing.; *C. pubescens* (Gillet) Kühner; *C. magnispora* (Murr.) Sing.; *C. siennophila* (Berk. & Br.) Sing. (*C. ochracea* Kühner ex Sing.); *C. kuhneriana* Sing.; *C. halophila* Sing.; *C. lentispora* Sing.; probably also *C. plumbeitincta* (Atk.) Sing.; certainly here: *C. fragilis* (Peck) Kühner (sensu Kühner) (*Galera incarnata* J. Schäffer); *C. fuscimarginata* (Murr.) Sing.; *C. rickenii* (J. Schäffer) Kühner (*Galera siliginea* (Fr. 1838 non anter.) Quél.); *C. umbellula* (Mont.) Sing.; *C. cylindracea* Maire & Kühn. ex Sing.

Note: If sect. *Conocybella* (Sing.) Watling is entered in *Conocybe* its place would be

\*c.n. (*Galera urticae* Velen., Novit. Myc., p. 131, 1939).

after sect. *Pilosellae*. It differs from the latter in the spores which are "dull fuscous in water mount when fresh, blackish when revived in KOH but fading" A.H. Smith; as in *Psathyrella* "the dark pigment can be dispersed by the application of concentrated sulphuric acid" but the resulting color is a "clear golden yellow" (Watling). The spores of the type did not impress me, in color, as possibly belonging to *Conocybe*, but their shape and the stipe covering are those of *Conocybe* sect. *Pilosellae*. The type and only species known is *P. michiganensis* A.H. Smith = *Conocybe michiganensis* (Sm.) Watling ("michiganense").

Sect. 5. *CANDIDAE* (Kühn.) Sing. Characters of the surface of the stipe as in section 4 but the whole stipe white, even at the base not distinctly pigmented.

Type species: *C. lateritia* (Fr.) Kühner sensu Kühner.

*C. lactea* (Lange) Métrod [Galera, Lange; *C. lateritia* (Batt. ex Fr.) Kühner sensu Kühner; *Agaricus* Batt. ex Fr. non Schaeff. ex Fr.; Galera, Kummer]; *C. subcrispa* (Murr.) Sing.; *C. crispella* (Murr.) Sing.; *C. subvelata* Sing. (possibly a separate section, perhaps *Singerella* Watl.?)

Sect. 6. *GIGANTEAE\** Sing. (1948). Characters of the surface of the stipe as in sect. 1 and 3 but the entire stipe white as in sect. 5. Stipe very stout for a *Conocybe*; assuming the habit of a *Cortinarius* or *Hebeloma*. Subtropical, also in Northern greenhouses.

*C. intrusa* (Peck) Sing. (*Cortinarius*, Peck; *Conocybe hebelomatoides* Middlehoek & Reijnders).

Subgenus II. *Ochromarasmius* Sing. (1947). Spores generally small, sometimes smaller than 6  $\mu\text{m}$ , distinctly warty or punctate from an exosporial ornamentation; stipe thin and sometimes rather firm, covered with numerous capitate dermatocystidia. On decayed stumps and chips, more rarely on the ground, or on needles.

Type species: *C. juruensis* (Henn.) Sing.

*C. juruensis* (Henn.) Sing.; *C. macrorhina* (Speg.) Sing.; *C. martiana* (Berk. & Curt.) Sing.; *C. missionum* Sing.; *C. radicata* Sing.; *C. dumetorum* (Velen.) Svrcek (Galera larinina Kühner).

### 153. **GALERELLA** Earle

*Bull. N. Y. Bot. Gard.* 5: 422. 1909.

Type species: *Agaricus coprinoides* Peck.

Characters: Differing from *Conocybe* in the non-capitate cheilocystidia and the plicate-sulcate pileus (after the manner of some thin Coprini); from *Bolbitius* in non-viscid pileus and smaller spores. On meadows and in woods and forests.

Development of the carpophores: Unknown.

\*Watling (1977, 1982) writes consistently "Gigantae".

*Area*: Temperate and subtropical, perhaps also tropical, regions of the northern and southern hemisphere.

*Limits*: See under *Conocybe*.

*State of knowledge*: Only one species is completely known. About this see Kühner, *Encycl. Mycol.* 7: 137-139. 1935, and Singer & Digilio, *Lilloa* 25: 309-312. 1951 (publ. 1952). Some other species are merely suspected to belong here.

*Practical importance*: Unknown.

## SPECIES

*G. plicatella* (Peck) Sing. (*Agaricus*, Peck; *Galera*, Earle; *Galerula*, Murr.; *Conocybe*, Kühner; *Agaricus coprinoides* Peck; *Galera*, Sacc.); according to Kühner probably also *Galera crocospora* (Berk. & Curt.) Sacc., *Galera pulchra* Clements, *Galera flava* Peck, and *Bolbitius coniocephalus* (Bull.) sensu Ricken.

*Note*: *G. plicatella* as understood here is so variable in some secondary characteristics, especially in South America, that it is possible that it will eventually be split into several "microspecies" or at least varieties.

### 154. PHOLIOTINA Fayod

*Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 359. 1889.

*Type species*: *Pholiota blattaria* (Fr.) Gillet (sensu Fr., Fayod).

*Syn.*: *Pholidotopsis* Earle, *Bull. N. Y. Bot. Gard.* 5: 443. 1909.\*

*Characters*: Characters as in *Conocybe*, but trama of the lamellae not of the *Conocybe*-type, but normally regular, i.e. with well developed mediostratum; spore print "Peruvian br." to "cocoa" or even brighter ferruginous (M & P); spores smooth, in two species ornamented (*P. subnuda* and *P. verrucispora*) and then with a marbled to verrucose surface (exosporium); cheilocystidia not abruptly capitate excepting in one section (3: *Intermediae*: four species); dermatocystidia present and then not necessarily capitate, or absent; veil often present, often annular and thick-membranous, even deeply sulcate and becoming free from the stipe in some species; hyphae with clamp connections, but occasionally without clamp connections (e.gr. *P. pygmaeoaffinis*, *P. mairei*). On foliage or decayed wood, on humus or earth, in and outside of woods and forests.

*Development of the carpophores*: Watling (1971, 1975) examined at least four species belonging to this genus, and stated paravelangiocarp for at least the exannulate species.

*Area*: Almost cosmopolitan.

\*Since in the American tradition *A. mycenoides*, the type species, is a *Pholiotina*, not a *Galerina*, *Pholidotopsis* is a synonym of *Pholiotina*.

*Limits:* See under *Conocybe*.

*State of knowledge:* The 24 species now listed under *Pholiotina* are well known; this is mainly due to Kühner's monograph (1935) and additional studies by the present author, some additional data given by Kitts van Waveren (under *Conocybe*) whose nomenclature is here accepted, as far as section *Pholiotina* is concerned, and a revision by Watling (1971).

*Practical importance:* One species contains psilocybin and is consequently considered to be hallucinogenic. Another contains  $\alpha$ -amanitin according to Brady, Benedict & Tyler (*Lloydia* 38: 172-173. 1975).

## SPECIES

Sect. 1. *PILIFERAE* (Kühner) Sing. Veil very indistinct, fibrillose-silky, fugacious, mostly not visible after primordial state has evolved; dermatocystidia generally present and projecting as filiform elements beyond the hymeniform epicuticular layer and there at times gelatinizing and surface of the pileus in this case subviscid to viscid; spores quite smooth with homogeneous wall; clamp connections often absent (but *C. aberrans* has clamp connections!); context not bluing when bruised. This section is the one most similar to *Conocybe* but differs in the cheilocystidia (not abruptly capitate) and the hymenophoral trama (not a *Conocybe*-structure).

*Type species:* *P. pygmaeoaffinis* (Fr.) Sing. (sensu Kühner).

*P. coprophila* (Kühner) Sing.; *P. aberrans* (Kühner) Sing.; *P. mairei* (Kühner) Sing.; *P. pygmaeoaffinis* (Fr.) Sing. (sensu Lange, Kühner; *Agaricus striaepes* Cooke).

Sect. 2. *CYANOPODAE* Sing. (1973). Psilocybin-producing species; carpophores staining blue (or green) in age or when bruised or touched; cheilocystidia not abruptly capitate; clamp connections present; veil poorly developed or absent.

*Type and only known species:* *P. cyanopoda* (Atk.) Sing.

Sect. 3. *INTERMEDIAE* (Watling) Sing. (1972). Cheilocystidia and dermatocystidia of the pileus capitate as in *Conocybe*; veil present, sometimes annuliform.

*Type species:* *Conocybe intermedia* (A.H. Smith) Watling.

*P. intermedia* (A.H. Smith) Sing.; *P. brunnea* (Lange & Kühner ex Watling) Sing.; *P. altaica* Sing.; *P. fibrillosipes* (Watling) Sing. ined. (*Naucoria appendiculata* Murr. ined. (?), non *Pholiotina appendiculata* (L. & K.) Sing.).

Sect. 4. *VERRUCISPORA* Sing. (1972). Cheilocystidia and dermatocystidia not abruptly capitate; spores ornamented (marbled to verrucose); veil not very distinct, early gelatinizing, or else none, except in the primordia; dermatocystidia on the pileus conspicuous or inconspicuous and rare; clamp connections present.

*Type species:* *P. verrucispora* Sing.

*P. subnuda* (Kühner) Sing.; *P. verrucispora* Sing.

Sect. 5. *PHOLIOTINA*. (*Togulares* Konr. & Maubl. 1924-27 ut sect. *Pholiotae* gen.). Cheilocystidia and dermatocystidia (where present) not abruptly capitate as in *Conocybe* or in sect. 3; spores quite smooth with homogeneous wall; veil present, often annuliform or appendiculate, if annuliform, the annulus often deeply sulcate and eventually separating from the stipe; pileus not viscid; context and surfaces of the carpophores not bluing when touched or bruised nor becoming blue or green in age; dermatocystidia on the pileus mostly absent, or inconsistent and few.

*Type species*: *P. blattaria* (Fr.) Fayod ex Sing. (sensu Fayod, Kitts van Waveren).

*P. blattaria* (Fr.) Fayod ex Sing. (sensu Fayod, Kitts van Waveren, Fr. non Ricken, non Kühner; *P. togularis* (Bull. ex Fr.) Fayod ex Sing. sensu Ricken, Kühner, Singer 1950-69 non Fr., Kitts van Waveren; *C. vexans* Orton); *P. teneroides* (Lange) Sing. (*C. blattaria* (Fr.) Kühner sensu Orton; *C. percincta* Orton); *P. tucumana* Sing.; *P. mycenooides* (Fr.) Sing. (sensu Kauffman, A.H. Smith); *P. rugosa* (Peck) Sing.\*; *P. filaris* (Fr.) Sing. (*Agaricus togularis* var. *filaris* Fr.; *Conocybe*, Kühner; *Galera vestita* var. *pusilla* Quél.; *Pholiota pusilla* (Quél.) Maire apud Kühner); *P. procera* Sing.; *P. arrhenii* (Fr.) Sing. (*Agaricus*, Fr.; *Pholiota*, Quél.; *Conocybe*, Kitts van Waveren; *C. blattaria* (Fr.) Fayod ex Sing. sensu Cooke, Ricken, Kühner; *Agaricus mesodactylus* Berk. & Br.); *P. vestita* (Fr. apud Quél.) Sing.; *P. peronata* (Kühner & Maire) Sing.; *P. appendiculata* (Lange & Kühner ex Watling) Sing.; *P. ruizlealii* Sing.; *P. aporos* (Kitts v. Waveren) Cléménçon.

## 155. DESCOLEA Sing.

*Lilloa* 23: 256. 1950 (publ. 1951).

*Type species*: *D. antarctica* Sing.

*Characters*: As in *Pholiotina* but spores never smooth, ellipsoid-amygdaliform or lemon-shaped, with verrucose to verrucose exosporial ornamentation, never nodulose, with an apical mucro, often snout-like, and an indistinct germ pore or more commonly callus, but never with a broad truncate germ pore, with complex wall and well developed perispore, ochraceous, golden ochraceous ("buff", "nugget", "antique gold" M & P) in print; pigments incrusting, mostly ocher-brown, melлеous-ochraceous or deep brown; hyphae with clamp connections; veil annuliform but also often showing strong remnants on pileus and stipe of a universal veil; lamellae adnexed or adnate and somewhat emarginate; cystidia none, but cheilocystidia mostly numerous, rarely sparse. On the ground among fallen leaves and woody particles or mosses, or on naked earth, more rarely on dead wood, mostly in the forest or at least near trees, not obligatorily ecotrophically mycorrhizal.\*\*

\*If indeed this and the following species are specifically identical as Kitts van Waveren (1970) suggests, the name to be accepted for the species *sensu lato* is *Pholiotina rugosa*, not *P. filaris*.

\*\*Horak assumed that the genus is ectotropically mycorrhizal, but this has not been demonstrated. At least *D. recedens* has been shown to be non-mycorrhizal since Singer M7218 (SGO) grew far from ectomycorrhizal trees and none of the trees accompanying it in typical anecotrophic forest had short-roots.

*Development of the carpophores:* "Hemiangiocarpous." Details unknown.

*Area:* South temperate zone and East Asia, according to Horak also in the Himalayas, possibly in North Africa.

*Limits:* The key characters separate this genus from other genera of the family; the combination of a well developed annulus, ochraceous spore print, and a hymeniform epicutis separate *Descolea* from the Strophariaceae and Cortinariaceae as well as the Crepidotaceae. See also note on limits of the family p. 542.

*State of knowledge:* The genus is now well known, after it has been studied thoroughly in South America from an anatomical as well as ecological point of view and after it has recently been revised by Horak (1971) who added four additional species to the four known to me and a key for the determination of all species.

*Practical importance:* Unknown.

## SPECIES

*D. antarctica* Sing.; *D. recedens* (Cooke & Mass.) Sing.; *D. pallida* Horak (the three preceding species perhaps too close to each other as now delimited); *D. flavoannulata* (Vassilieva) Horak; according to Horak also *D. majestatica* Horak; *D. pretiosa* Horak; *D. phlebophora* Horak; *D. gunnii* Horak; according to description and figures also *Naucoria rheophylla* Bert. & Mal..

## 156. BOLBITIUS Fr.

Epicrisis p. 253. 1838.

*Type species:* *B. fragilis* (L. ex S.F. Gray) Fr.\*

*Syn.:* *Pluteolus* (Fr.) Gillet, *Hymenom. Fr.* p. 549. 1876.

*Agaricus* subgenus *Pluteolus* Fr., *Hym. Eur.* p. 266. 1874.

*Mycena* (Pers.) Roussel ex Murr., *North Amer. Fl.* 10: 190. 1917 non (Pers. ex Fr.) S.F. Gray (1821).

*Characters:* As in the family, but differing from the other genera of the Bolbitiaceae in sulcate-plicate or pectinate margin, combined with an opimus to viscid surface of the pileus; cheilocystidia not abruptly capitate; stipe usually white, more rarely pink; clamp connections present or absent; spores smooth, with broad truncate germ pore, in print either bright ferruginous as in *Conocybe* or more brown as in *Agrocybe* (for example "Cochin" M & P); lamellae sometimes weakly deliquescent; on dung, on humus, or on earth, inside and outside the woods and forests, also on rotten trunks of trees, on swampy or sandy soil, sawdust, etc.

*Development of the carpophores:* Hemiangiocarpous: paravelangiocarpous, almost

\* Other authors have selected as lectotype of the genus: *B. vitellinus* respectively *B. titubans*; the selection is irrelevant from a taxonomical point of view since all three species are identical or extremely closely related.

*gymnangiocarpous* according to Reijnders; *hymenocarpous*. Watling (1975) confirmed Reijnder's findings.

*Area:* Probably almost cosmopolitan.

*Limits:* Kühner (1935) sums up the differences between this genus and *Conocybe*, *Galerella*, and *Pholiotina* in the following manner: "It differs from [these genera] at first in the viscid covering of the pileus. The *Bolbitii* which have a pileus that is almost always striate or even split above the dorsal part of the lamellae like that of the veliform *Coprinis*, appear to be generally lacking the brownish ocher membranapigment which is present especially in the lower portions of the stipe in nearly all species of *Conocybe* [*Galerella*, and *Pholiotina*]; their stipe is white to the base unless it shows - as is very often the case in the pileus - such bright colors as yellow, greenish bluish, violet, or rose; these colors are intracellular, at least in *Bolbitius titubans* and *B. aleuriatus* whereas the *Conocybes* [*Galerellas* and *Pholiotinas*] generally appear to lack all vacuolar pigment. The *Bolbitii* are separated from *Conocybe* anatomically by their [homogeneously] regular [hymenophoral] trama and by the pseudoparaphyses which are often more developed."

Since there are species in *Bolbitius* which have dull brown (not really rusty) spore print, for instance one species collected by the author in Virginia with "Cochin" (Maerz & Paul) spore print on white paper (perhaps *B. nobilis* Peck), there is also need of separating *Agrocybe* from *Bolbitius* on the basis of other characters than the color of the spore print. However, the distinguishing characters indicated in the generic key will be sufficient in all cases to avoid confusion between the two genera.

*State of knowledge:* The genus *Bolbitius* is comparatively little known. It has been monographed only for restricted areas and in connection with related genera. The distinguishing features of the European species are very weak. In other parts of the world where there are many more species of *Bolbitius*, the situation is even worse. In the eastern states of the U.S.A., several species can be found which appear to be omitted in the floras, and will probably turn out to be new. A monograph of the American species is most urgently needed. 13 species are considered as belonging in *Bolbitius*.

*Practical importance:* None.

## SPECIES

*Stirps Reticulatus.* (On wood; usually without yellow or pink pigment and not entirely white; spore print bright ochraceous rusty.)

*B. reticulatus* (Pers. ex Fr.) Ricken; *B. aleuriatus* (Fr.) Sing. (*Pluteolus*, Karst.).

*Stirps Vitellinus.* (On pastures, on dung or sawdust, etc., often white or yellow, or pink; spore print bright ochraceous rusty or dull argillaceous-brown.)

*B. vitellinus* (Pers. ex Fr.) Fr. [*Bolbitius fragilis* (L. ex Fr.); *Bolbitius titubans* (Bull. ex Fr.) Fr.]; *B. mesosporus* Sing.; *B. albus* (Peck) Watling; *B. albiceps* Speg.; *B. demangei* (Quél.) Sacc. & Sacc. (*B. incarnatus* Hongo); *B. tucumanensis* Sing.

According to Kühner, the following species also belongs in *Bolbitius*: *B. glauco-purpureus* (Berk. & Br.) Kühner ]*Agaricus* (Galera), B. & Br.].

According to Murrill, the number of species in *Puteolus* and *Bolbitius* as cited in *North America Flora* 10: 186-193. 1917, is twenty-seven. Some of those apparently representing true *Bolbitii* are: *Pluteolus glutinosus* Clements; *Mycena variicolor* (Atk.) Murr. (recte: *Bolbitius variicolor* Atk.); *Pluteolus coprophilus* Peck (recte *Bolbitius coprophilus* (Peck) Hongo); *P. flavellus* Murr., and *P. brunneidiscus* Murr. (recte *Bolbitius brunneidiscus* (Murr.) Sacc. & Trotter). Of them, I have studied material fitting the descriptions but not compared with the types.

### 157. AGROCYBE Fayod

*Prodrome, Ann. Sc. Nat.* VII. 9: 358. 1889.

*Type species: Pholiota praecox* (Pers. ex Fr.) Quél. (sensu Fayod).

Syn.: *Cyclopus* (Quél.) Barbier, *Bull. Soc. Sc. Nat.*, Saône-et-Loire II. 33: 131. 1907.

*Togaria* W.G. Smith, *Brit. Basid.* p. 122. 1908 [typus *T. dura* (Bolt. ex Fr.) W.G. Smith\*] em. Romagnesi, *Rev. Mycol.* 2: 178. 1937.

*Bulla* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 424. 1909.

*Pseudodeconica* Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 19. 1927, nom. nud.

*Cyclocybe* Velen. ex Velen., *Nov. myc.* p. 122. 1939.

*Characters:* Pileus comparatively fleshy, not sulcate-plicate but either entirely estriate or very finely transparently striate over a very short distance from the margin toward the center, with a hymeniform covering forming the epicutis and consisting of globose or short-piriform cells; lamellae broad (moderately broad to extremely broad), either with cystidia on both the sides and the edge of the lamellae or with cheilocystidia only; basidia 2-3-, or 4-spored, otherwise normal; spore print 14-H-10 to "kis kilim", "Cochin", "burnt umber", "chocolate", "Montella", "Mandalay", "Cocoa" or even darker in the same tone, "partridge", "Conga" (Maerz & Paul); spores under the microscope melleous usually with a deep chestnut ferruginous line, smooth, with thick double wall, with germ pore (which is either broad and truncate or narrow and non-truncate, and then often easily overlooked and indistinct), rarely spore wall at apex completely continuous, in some species with a majority of pore-less spores in a print, in other species spores with 2-3 germ pores occasionally observed; stipe white or colored, smooth or rough-fibrillose, with or without veil, the latter often well developed and leaving an annulus on the mature stipe, base of the stipe often with thin, white rhizomorphs (rhizoids); sometimes forming sclerotia; context consisting of hyphae with clamp connections, rarely clampless. In the woods and outside the forested areas, often in gardens or lawns, on sand dunes, fields, and meadows, on dung, seeds, rotting *Cormophyta* including decaying wood, also in greenhouses on manured soil, on anthills.

*Development of the carpophores:* "Hemiangiocarpous." According to Reijnders

\*W.B. Cooke (1953) indicates as type "*T. aurea* W.G. Sm." - a choice of lectotype which must be rejected after Romagnesi's emendation of the genus with exclusion of *P. aurea*. W.G. Smith did not designate a type species for this genus.

(1963) paravelangiocarpous, hymenocarpous, at least in *A. praecox* and related species. However, *A. aegerita* is bivelangiocarpous because of the presence of [primary] angiocarp from a universal veil which is apparently absent in subgenus *Agrocybe* (Reijnders 1971); in this species the sequence of development is pileo-stipitocarpous. Aside from the primary angiocarp, the occurrence of secondary angiocarp in *A. aegerita* is quite noteworthy. It explains the position of the annulus in the upper part of the stipe. In this case even the hymenophore contributes to the formation of the annulus. Watling (1975) has examined several species of this genus and, like Reijnders, found paravelangiocarpous development in some sections (but doubts whether this finding applies to section *Velatae*).

**Limits:** See under "limits" after the description of the family (p. 541). The striking difference between *A. aegerita* and *A. praecox* as far as their developmental characters are concerned might suggest that the genus is heterogeneous. From a chemical, anatomical and macromorphological point of view, this is not the case. It should be taken into consideration that paravelangiocarpous and bivelangiocarpous species exist side by side also in other basically homogeneous genera like *Psathyrella*.

**State of knowledge:** Although recent investigations by the present author have shed some light on the taxonomy of such difficult groups as that of *A. pediades*, and the majority of the species are now considered well known - 53 of these are enumerated below - the genus is still in need of a monographic treatment. A careful evaluation of the veil characters and biometrical data on spore development and length-to-breadth relation (Q)\* might be helpful as well as further studies on carpophore development.

**Practical importance:** Several species of *Agrocybe* are excellent edible mushrooms. Some have been cultivated by primitive methods in Southern Europe, and *A. aegerita* is often sold in the markets, especially in Italy and Chile. *A. dura* and *A. praecox* can be cultivated on a mixture of barley chaff and sawdust (Kersten, *Zeitschr. f. Pilzk.* 6 (n.s.): 5-9, 1950) and *A. aegerita* has been cultivated in California (Bob Harris, "Mushroom people") together with other lignicolous agarics. "*A. dura*" (probably *A. vermisflua*) contains an antibiotic, agrocybin (Kavanagh et al., *Proc. Nat. Acad. Sc. Wash.* 36: 102-106. 1950).

## SPECIES

**Subgenus Agrocybe (*Eu-Agrocybe* Sing. 1936).** Spores either distinctly truncate and with broad germ pore, or scarcely truncate and with very narrow germ pore; carpophores developing paravelangiocarpously (as far as known); veil present or absent; mostly not lignicolous, more rarely on decayed wood; clamp connections present.

**Type species:** *A. praecox* (Pers. ex Fr.) Fayod ex auct. (sensu Fayod).

**Sect. 1. PEDIADEAE (Fr.) Sing. (1936).** Veil usually none, rarely flocculose on the margin of the pileus, exceptionally thinly membranous and even annuliform but

\*cf. Singer, *Trud. Bot. Inst. Kom. Akad. Nauk SSSR* II 6: 446-462. 1950.

very fugacious; pleurocystidia generally absent, rarely present but very inconspicuous and scattered and then spores (as in most species)  $> 11.5 \mu\text{m}$ .

Type species: *A. pediades* (Pers. ex Fr.) Fayod ex auct.

*A. pediades* (Pers. ex Fr.) Fayod ex auct.; *A. semiorbicularis* (Bull. ex St-Amans) Fayod ex auct. (constantly 2-spored: sensu Sydow); *A. fimicola* (Speg.) Sing. (Naucoria subamara Murr. p.p.); *A. coprophila* Sing. non (Rick) Sing.; *A. arenicola* (Berk.) Sing.; *A. media* Hongo; *A. arenaria* (Peck) Singer\*; *A. cubensis* (Murr.) Sing.; *A. sacchari* (Murr.) Dennis (Naucoria, Murr.); *A. insignis* Sing.; *A. platysperma* (Peck) Sing.; *A. lenticeps* (Peck) Sing.; *A. subpediades* (Murr.) Sing.

Sect. 2. *AGROCYBE*. (*Praecoces* (Konr. & Maubl. as section of *Pholiota*) Sing. 1936. Veil well developed and forming an annulus, more rarely present only as floccos on the margin; cystidia on the sides of the lamellae numerous and conspicuous; spores with a broad, truncate germ pore.

Type species: *A. praecox* (Pers. ex Fr.) Fayod ex auct. (sensu Fayod\*\*).

*A. puiggarii* (Speg.) Sing.; *A. perfecta* (Rick) Sing; *A. platensis* (Speg.) Sing.; *A. alachuana* (Murr.) Sing.; *A. vermisflua* (Peck) Watling; *A. molesta* (Lasch) Sing.; *A. recalva* (Lasch) Sing.\*\*\*; *A. paludosa* (Lange) Kühn. & Romagnesi; *A. howeana* (Peck) Sing.; *A. sphaleromorpha* (Bull. ex Fr.) Fayod ex auct. sensu Sing. 1977, Bon, Watling vix Secr., Moser and Bull. ex Fr. (possibly a race of *A. recalva*); *A. praecox* (Pers. ex Fr.) Fayod ex auct. (non sensu Fayod); *A. acericola* (Peck) Sing.; *A. gibberosa* (Fr.) Sing. (sensu Sing.); *A. viscosa* Sing.; *A. broadwayi* (Murr.) Dennis; *A. earlei* (Murr.) Dennis ex Sing.; *A. splendida* Cléménçon\*; *A. hortensis* (Burt) Sing. (exannulate!).

Sect. 3. *MICROSPORAE* Sing. (1936). Veil none; cystidia on the sides of the lamellae present and conspicuous or spores not larger than  $13 \mu\text{m}$ , mostly smaller than  $10 \mu\text{m}$ , spores with a broad, truncate germ pore.

Type species: *A. tuberosa* (Henn.) Sing.

*A. arvalis* (Fr.) Sing. (*A. tuberosa* (Henn.) Sing.; Naucoria temulenta (Fr.) Kummer sensu Heim & Romagnesi non Fr.; Agrocybe Sing.; Galera arvalis var. tuberigena Quél.; Naucoria sclerotina Velen.) with var. *heterospora* Sing.; *A. putaminum* (Maire) Sing.; *A. sororia* (Peck) Sing.; *A. amara* (Murr.) Sing.; *A. farinacea* Hongo (the latter two possibly but varieties of *A. sororia*); *A. retigera* (Speg.) Sing. (Naucoria semiorbicularis var. lacunosa Murr.); *A. collybiiformis* (Murr.) Sing.; *A. neocoprophila* Sing. (*A. coprophila* (Rick) Sing. non *A. coprophila* Sing.); *A. broad-*

\*A study of the types of both *A. splendida* and *A. arenaria* (Peck) Sing. has shown the two species to be very similar but differing in the rather numerous pleurocystidia in the former and the extremely scarce, often absent pleurocystidia in *A. arenaria*. *A. platysperma* also has extremely few or no pleurocystidia and much broader spores than *A. splendida*; also its pileus is paler and larger.

\*\*Specimens so determined by Fayod (G) are consistently = *A. molesta* (Lasch) Sing.

\*\*\*c.n. (*Agaricus recalvus* Lasch, *Linnaea* 3: 421. 1828).

*wayi* (Murr.) Dennis (Hebeloma, Murr.); *A. procera* Sing.L; also *A. manihotis* Pegler.

Sect. 4. *ALLOCYSTIDES* Sing. (1975). Differing from sections 1-3 by capitate, eventually thick-walled cystidia which are numerous and conspicuous on the sides of the lamellae; epicutis often early disintegrating. On dung. Annulus very incomplete and mostly absent but veil often abundant; spores with a broad, truncate germ pore.

Type and only known species: *A. allocystis* Sing.

Sect. 5. *EVELATAE* Sing. (1948). Veil none or fugacious (marginal or subannular); differs from sections 1-4 in a narrow, incomplete, or at least not truncate germ pore which may be entirely absent in some spores, or somewhat truncate in others. Cystidia present or absent on the sides of the lamellae; spores always less than 10  $\mu\text{m}$  long. Differs from subgenus *Aporus* in the absence of an annulus and mode of development.

Type species: *A. firma* (Peck) Sing.

*A. vervacti* (Fr.) Romagnesi (sensu Lange, Kühner & Romagnesi); *A. carelica* Sing. (*Naucoria sobria* (Fr.) Kummer sensu Höhn., herb. FH); *A. xerophytica* Sing.; *A. xuchilensis* (Murr.) Sing.; *A. firma* (Peck) Sing.; *A. illicita* (Peck) Watling; *A. pruinatipes* (Peck) Watling (the latter two may be too close to *A. firma*); possibly also *A. pusiola* (Fr.) Heim. and *A. attenuata* (Kühn.) Orton.

Subgenus *Aporus* Sing. (1936). Spores without a germ pore or with a narrow, exceptionally (in some spores) broad, generally not, exceptionally distinctly truncate germ pore; carpophores developing bivelangiocarpously (as far as known); veil annular; on earth, humus, or wood (including living or freshly cut trunks); clamp connections present or absent; pleurocystidia always conspicuous. Pl. 42.

Type species: *A. aegerita* (Brig.) Sing.

Sect. 6. *VELATAE* Sing. (1936). Germ pore of the spores practically absent; clamp connections present or absent. Humicolous or terricolous species. Rather dark-colored small to medium sized carpophores; rarely more lightcolored and then spores small (<9 $\mu\text{m}$ ).

Type species: *A. erebia* (Fr.) Kühner.

*A. erebia* (Fr.) Kühner and allied species such as *A. aggericola* (peck) Sing., *A. washingtoniensis* (Murr.) Watling.; *A. brunneola* (Fr.) Watling, and *Pholiota indecens* Peck; also *A. lazoi* Sing.

Sect. *APORUS* (Sing.) Sing. (*Aporus* Sing. [subg. sensu stricto, st. n.]) On wood of dead and living trees; hyphae with clamp connections. Large, generally light colored (pallid to gilvous, ochraceous, isabelline), fleshy carpophores; germ pore of the spores variously developed, narrow and non-truncate or even absent to moderately broad and somewhat truncate. Pl. 42.

Type species: *A. aegerita* (Brig.) Sing.

*A. aegerita* (Brig.) Sing. (*Pholiota cylindracea* Gillet; ?*Agaricus cylindricus* "D.C.

ex Fr."\*\*; *Pholiota crassivela* (Speg.) Sacc.; *P. impudica* Speg.; *P. phyllicigena* (Berk.) Sacc.; *Agaricus poppiarello* Viv.).

**Note:** This is probably a collective species or "linnaeon" since I have observed a considerable variability of the cystidial characters (often with acuminate, subfusoid cystidia), bi- and tetrasporous forms, and forms with reticulately venose-rugose pileus. Also, the cultural characters are not fully uniform.

## STROPHARIACEAE Sing. & Smith

*Mycologia* 38: 503, 1946; Van Overeem, *Bull. Jard. Bot. Buitenzorg* 9: 19. 1927 (*nom. nud.*); Romagnesi, *Rev. Mycol.* 2: 243. 1937 (*nom. nud.*).

**Type genus:** *Stropharia* (Fr.) Quél.

**Characters:** Epicutis of the pileus either consisting of thin hyaline filamentous, clamped, strictly repent hyphae or else these hyphae are bundled together and ascendant to form scales, or they form a trichodermium, even (if consisting of short articles) a sort of epithelium, but in case they form a trichodermium or epithelium, the component elements are broad, firm- to thick-walled, and crystalline-incrusted or colored by a strong intraparietal pigment and incrusted by pigment; hypodermium often subcellular; hymenophore lamellate; lamellae adnexed, sinuate, adnate, or adnate-decurrent, very rarely subfree (never quite free); spore print deep lilac to blackish lilac, or else cinnamon brown, deep rusty cinnamon, or deep fuscous-sepia with, perhaps, a slight purplish hue more rarely more intensely ferruginous or as light colored as yellow-ochraceous (for more precise color indication see in the different genera!); spores under the light microscope smooth, very rarely slightly marbled or indistinctly punctulate, melleous to chestnut, more rarely ferruginous (KOH), often with a deep reddish chestnut reflex around the endosporium, the wall always well differentiated into endo- and episporium and rarely continuous at the apex, usually with a more or less broad germ pore and often distinctly truncate, normally binucleate, hilum with open-pore structure (Pegler & Young); cystidia present only on the edges (cheilocystidia), or else also scattered to numerous on the sides of the lamellae, in the latter case, they belong frequently to a special type of cystidia, called chrysocystidia (Pl. 21), with an amorphous body in the broadest portion of the cystidium, this body turning more or less strongly yellow in NH<sub>4</sub>OH, the shape of the chrysocystidia always characteristic, clavate or clavate-mucronate; context always soft-fleshy and not light in weight and dry, never tough, but often bitter to the taste; all hyphae with clamp connections. On a great variety of substrata, in deep moss, on living or decayed wood, on charcoal, on living Pteridophyta, on foliage and needles, on palm detritus, dead Gramineae and other

\*Fries (1821, p. 247), under an invalid specific Michelian name (Art. 23.6c) mentions as "forsan mere formae" four pre-1821 species published by De Candolle, among them "*b. A. cylindricus*" [D.C.] which probably belongs in the complex *Agrocybe aegerita*. When he accepts *A. aegerita* in 1838, he does not mention his earlier quotation but merely indicates a likewise invalid fungus name and plate by Battara which he had judged to be probably leucosporous. *A. cylindricus* is also illegitimate according to Art. 34 of the Code. Other 1821 republications are dubious including Mérat's of *A. pudicus* Bull.

herbaceous stems, fruits, etc., on living grass roots, exposed tree roots, on dung, and on the earth; in open fields, pastures, gardens, etc., and also in the woods, hammocks, tundras, and swamps; not ectomycorrhizal.

**Limits:** This family is very well delimited from the other families with colored spores; the taxonomic difficulties clearly expressed in previous papers by me and becoming obvious in Smith & Hesler's (1969) *Pholiota* monograph, are those of subdivision, not delimitation.

Clampless *Stropharia*- or *Pholiota*-like fungi like *Pholiota fulvosquamosa* Peck as described by Smith & Hesler (p. 184) are likely to belong in the same group as *Stropharia kauffmanii* which was discussed under *Agaricus* (p. 485); they are certainly not strophariaceous fungi. The presence of clamp connections in the trama of the carpophores is as constant as in any taxon of Agaricales and so is the lack of ectotrophic associations, the lack of hymeniform epicutis structures, the absence of truly free lamellae, and verrucose spores.

The genus *Phaeomarasmius* - with some misgivings and hesitation - had been attached to the family Cortinariaceae where it has so little affinity that it was put in a special tribus. Even if Smith & Hesler's treatment of the bulk of the species of that genus (and tribus) - excepting the type species - suggested that the affinity to certain groups of *Pholiota* is stronger than that to other genera of Cortinariaceae, I cannot agree to the inflated genus concept of *Pholiota* which, aside from all Pholiotoideae also contains the Phaeomarsmieae, elements of *Stropharia* and *Naematoloma*, with a fleeting link with *Psilocybe*, and even the genus *Phaeolepiota* which is totally foreign to the family Strophariaceae. As for *Phaeomarasmius*, we (Machol & Singer 1972) have used a quantitative technique in order to establish whether this genus, according to its known characters, is closer to the Pholiotoideae or the Cortinarieae or Inocybeae (Cortinariaceae), and the result showed convincingly that the affinity with the former was strongest. This includes likewise the relationship of *Phaeomarasmius* with the Crepidotaceae. For more details see under *Phaeomarasmius*.

The Galeropsidaceae (*Galeropsis*, *Weraroa* = *Clavogaster*, etc.) differ from the Strophariaceae (which I believe derived from them) by having apobasidia and not producing a spore print.

The Cortinariaceae proper differ from the Strophariaceae in either being non-ectomycorrhizal but with generally  $\pm$  ornamented spores, or ectomycorrhizal with smooth or ornamented spores. For the delimitation of the genera of these families, see there.

#### KEY TO THE SUBFAMILIES

- A. Spore print deep lilac, fuliginous lilac (and then spores when seen in fresh condition mounted in water-lilac, amethyst or livid) or a deep fuscous warm sepia, purplish brown (e.gr. "Rosetta", "moose", 8-C-3, "Java", "casserole", "blue fox", 8-H-3, 8-E-2, 8-A-4 M. & P.); spores in alkaline solutions often turning deeper chestnut, olive, or with a chestnut or brown-red reflex (seen when the spores are slightly out of focus for the optical section, along the endosporium), sometimes lentiform

or with rhombic outline in frontal view, generally with a distinct broad, more rarely narrow, germ pore; sometimes containing psilocybine or psilocin and then bluing in some parts either in age or on touching or bruising, particularly in the stipe (*Naematoloma*, sect. *Cyanoloma*; *Psilocybe*, sect. *Caerulescentes*).

*Stropharioideae*, p. 558

- A. Spore print more brown\* (cinnamon brown, rusty brown, even bright cinnamon or cinnamon-ochraceous, yellowish ochraceous, light ochraceous, rusty ochraceous, bright ferruginous, often argillaceous-brown or tobacco brown, under the microscope melleous-ochraceous, melleous-brown, tawny-brown, with or without a germ pore, rarely and then indistinctly lentiform and rarely with a rhombic outline when seen frontally; not containing psilocybin or psilocin as far as known, and not bluing when bruised.

*Pholiotoideae*, p. 574

### Subfamily *Stropharioideae* (Sing.) Sing.

Lilloa 22: 497. 1951.

Type genus: *Stropharia* (Fr.) Quél. = *Stropharia* Kummer.

Syn.: *Coprinaceae* subfam. *Stropharioideae* Sing., Ann. Myc. 34: 340. 1936.

*Nematolomeae* Fayod, Ann. Sc. Nat., Bot. VII. 9: 369 (tribus Nematolomés).

*Stropharieae* Konr. & Maubl., Ic. Sel. Fung. 6: 92. 1924-37 (Strophariés).

Characters: See key above.

Note: Though this subfamily was originally based on a single character viz. the color of the spore print, it seems to be a natural unit because the principles of subdivision into genera are different in the subfamilies. It appears therefore that the evolution within these parallel series has taken place according to the development of different characters in a different sequence. Since the genera composing the *Stropharioideae* and those composing the *Pholiotoideae* are by no means completely parallel but only roughly comparable, the color of the spore print must remain the leading character, with the modifications pointed out under the heading "Limits" in genera 158-160. Some modern authors have found the real or apparent difficulties of delimiting and defining the genera of the subfamilies *Stropharioideae* and *Pholiotoideae* too overwhelming and have resigned themselves to recognize a single genus in each. Not only does this attitude not solve the problems, but the keys to the genera of each subfamily as given below (and since 1975) present, according to the author's experience, a solution to all difficulties encountered.

### KEY TO THE GENERA

- A. Chrysocystidia typically present (with yellow internal amorphous body visible in alkalic solutions; this body strongly colorable in cotton blue mounts; shape of the chrysocystidia broadly ventricose-clavate and mucronate, more rarely non-mucronate, generally quite thin-walled, both on edges and sides of the lamellae, often accompanied by endocystidia of the chrysocystidial type; pileus mostly not or only partly hygrophanous, centrally stipitate.

\*Rarely a deep chocolate color and then apical germ pore of the spores poorly developed, narrow and non-truncate. Non-coprophilous species with spores not lilac when seen fresh in water, having a glutinous sheath over the stipe, should be looked for in *Pholiotoideae*. Otherwise, a spore print near or between "cocoa" and "clove" (M&P) should be interpreted as indicating *Stropharioideae*.

B. Stipe annulate; hypodermium not forming a subcellular layer \*; hymenophoral trama regular but of hyphae with unequal diameter and tending to be or become interwoven; generally not fascicular, often growing on the soil in meadows or on dung (but also lignicolous and on various débris in the forests).

158. *Stropharia*, p. 559

B. Stipe without an annulus, or if exceptionally with an annulus, fungi not combining the characters indicated above.

C. Hypodermium not forming a subcellular layer; hymenophoral trama not of persistently parallel hyphae; pileus more or less thoroughly hygrophanous; never growing fascicularly and habit almost omphaloid (see "E" below).

C. Hypodermium forming a subcellular layer, consisting of noticeably short cells not of elongated hyphal cells organized into parallel horizontal chains; hymenophoral trama of parallel hyphae, those of the mediotrastum often inflated but not or little interwoven; pileus only partly (on margin) or not or scarcely hygrophanous; often growing in fascicular accumulations on wood (but also singly on earth, débris, humus, in deep moss etc.).

159. *Naematoloma*, p. 562

A. Chrysocystidia absent.

D. Stipe centrally attached and usually rather long in relation to the diameter of the pileus.

E. Hypodermium distinctly subcellular; annulus well developed, white, membranous; or else hypodermium not at all subcellular and then annulus entirely continuous by glutinous (entire stipe covered by a glutinous layer)

F. Hypodermium distinctly subcellular; annulus not gelatinized; lignicolous or on woody débris in the woods and forests (see "C" above: *Naematoloma*).

F. Hypodermium not subcellular; stipe glutinous from the veil; on manured meadows, pastures, often on dung (see *Stropharia*).

E. Not with subcellular hypodermium; not with glutinous annulus. 160. *Psilocybe*, p. 565

D. Stipe eccentric and short in relation to the pileus, mostly curved. 161. *Melanotus*, p. 573

## 158. STROPHARIA (Fr.) Quél.

*Champ. Jura Vosg.*, p. 141. 1872-3.

Type species: *S. aeruginosa* (Curt. ex Fr.) Quél.

Syn.: *Agaricus* trib. *Stropharia* Fr., *Summ. Veg. Scan.*, p. 295. 1849.

*Geophilus* Quél., *Enchiridion*, p. 111. 1886, non D. Don (1825).

*Psalliota* subgenus *Stropharia* (Fr.) Schröter in Cohn, *Krypt. Fl. Schles. Pilze* 1: 537. 1889.

*Stercophila* Romagnesi, *Rev. Mycol.* 1: 36. 1936 (*nom. nud.*).

Characters: Pileus humid or viscid often white or bright-colored (red, yellow, fulvous, etc.); epicutis consisting of repent filamentous hyphae; hypodermium not subcellular; lamellae adnexed to adnate, usually broad; trama regular but becoming irregular in age; chrysocystidia present (Pl. 22), rarely absent, and then the stipe covered by a glutinous veil; cheilocystidia always present and well differentiated making the edge of the lamellae heteromorphous; spore print lilac to fuliginous-lilac (within the colors indicated for the subfamily Stropharioideae in the key) varying to purplish fuscous and sometimes becoming duller colored when slowly dehydrated in the herbarium, usually lilac or livid when seen in water in fresh condition, with thick, complex, smooth wall and with an often distinctly truncate germ

\* In determining whether a true subcellular hypodermium is present it must be made certain that its elements are subcellular (and not running perpendicularly to the plane of the objective) and that they are located immediately underneath the epicutis (rather than in an infrahypodermal, often ± pigmented) layer of the trama of the pileus which, in some cases, may contain many short cells.

pore; stipe central, annulate, but in some species stipe coated by an entirely glutinous veil consisting of a gelatinous mass with a few filamentous hyphae imbedded; tissue culture and basal mycelium typically producing acanthocytes (see p. 4), except (all?) species of sect. *Stercophila*. On the soil and foliage, on wood or sawdust, on dung, in and outside the wooded areas.

*Development of the carpophores:* Bivelangiocarpous and probably always hymenocarpous (according to the data given by Reijnders).

*Area:* Almost cosmopolitan (not in Antarctica).

*Limits:* The delimitation of the genus is not difficult as far as the genera of its subfamily are concerned, if the key characters are carefully checked. If the affinities of the species are considered, it is obvious that the species with glutinous stipe but lacking chrysocystidia cannot be separated from those that have them. On the other hand, all those species without a glutinous stipe but likewise lacking chrysocystidia belong to *Naematoloma* (if the hypodermium is subcellular) or *Psilocybe* where they are closely related to exannulate species. For this reason, such occasionally annulate species as *P. merdaria* and allies and such annulate species which belong in the bluing, psilocybin-containing group, are here excluded from *Stropharia*. Small hygrophanous species without annulus, even if they have chrysocystidia, are likewise considered as *Psilocybe* (as is done by all modern authors). In this manner, *Stropharia* is restricted to a natural group, relatively easily definable and separable from the rest of the genera.

Much more difficulty is encountered when a clear separation of stropharioid genera from pholiotoid genera is attempted, and the separation of *Stropharia* from *Pholiota* has caused some authors to doubt the possibility of relying on the spore print color alone. In the present arrangement I have made the affinity of the ambiguous species (such as *Pholiota johnsoniana*, *P. malicola*, *P. myosotis*) the basic motive for their position and have the diagnoses of the genera and the wording of the keys adapted to this principle. Once this position is understood, it will also be understood that the species with chrysocystidia and a narrow non-truncate germ pore on the spores are now relegated to *Pholiota* where we have sections or subsections with a certain amplitude of spore print colors. By accepting Smith & Hesler's disposition of *Pholiota johnsoniana*, it can be avoided that an otherwise continuous series between that species and *Pholiota* section *Albivelatae* had to be broken and divided between the genera *Stropharia* and *Pholiota*. By the same token, all those species with glutinous stipe, as long as they have no affinity with *Stropharia* section *Stercophila*, are transferred to or left in *Pholiota* subgenus *Phaeonematoloma*. Naturally, also those species which are devoid of chrysocystidia but do not fit into either *Psilocybe* or *Stropharia* subgenus *Stercophila* or *Naematoloma* sect. *Stropholoma* are placed in *Pholiota* as long as affinity with groups of that genus can be established, even if the spore color is different from the normal spore color in shade or tonality. Thus, *Pholiota malicola*, as has been shown by Smith & Hesler, shares the pseudoamyloid spores with *Pholiota* section *Flammula* and is closely related to the other species of that group. For a similar reason, I cannot agree that *P. albocrenulata* is related to *Stropharia* rather than *Pholiota* sect. *Albocrenulatae*.

Even though the delimitation between *Stropharia* and *Pholiota* is now rather satisfactory, natural and sharp, the taxonomist who attempts to determine a strophariaceous species without having a fresh spore print at hand is strongly advised to compare the sections and species of both the stropharioid and pholiotoid series.

**State of knowledge:** The genus is comparatively well known but there is no doubt but that monographic studies, especially in non-European countries will prove the existence of many undescribed species. Many valuable contributions to the knowledge of this genus were made indirectly (discussing the limits between *Naematoloma* and *Stropharia*) by R. Kühner, and many more species were described as new, or redescribed by A.H. Smith in North America. The author limits the list of species admitted in the sections indicated below, to 14.

**Practical importance:** Though some of the species are considered as edible, they are not eaten much, with the exception of *Stropharia rugosoannulata* which was successfully grown for food in the German Democratic Republic on straw-filled beds in the open and is now being cultivated in several countries.

## SPECIES

Sect. 1. *MUNDAE* (Fr.) Konr. & Maubl. (1924-37). Pileus subviscid or merely humid, never strongly viscid or glutinous. Annulus deeply grooved. In and outside the woods and forests, mostly on earth.

*Type species:* *S. coronilla* (Bull. ex Fr.) Quél.

*S. melanosperma* (Bull. ex) Quél.; *S. coronilla* (Bull. ex Fr.) Quél.; *S. pendolae* (Speg.) Sing.; *S. rugosoannulata* Farlow apud Murr. (*S. ferrei* Bres.).

Sect. 2. *STROPHARIA* (*Pholiotidei* Fr. 1836 ut sect. *Agarici* trib. *Psalliota*, em. Sing. 1951; *Viscipelles* Fr. 1854; *Aeruginosae* Fayod 1889). Pileus subviscid to glutinous; carpophores often growing in the woods, on débris, under ferns, in shady places in parks etc.

*Type species:* *S. aeruginosa* (Curt. ex Fr.) Quél.

*S. aeruginosa* (Curt. ex Fr.) Quél.\*; *S. inuncta* (Fr.) Quél.; *S. albonitens* (Fr.) Karst.; *S. hornemannii* (Fr. ex Fr.) Lundell & Nannfeldt [*Naematoloma*, Sing. 1951]; *S. depilata* (Pers. ex Fr.) Karst.]; *S. viloriana* (Dennis) Sing.; *S. flocculipes* Sing.; *S. andina* Sing.; apparently also *Pholiota sipei* Smith & Hesler.

Sect. 3. *STERCOPHILA* (Romagnesi) Sing. Pileus viscid to glutinous; stipe also glutinous from an entirely glutinous, more rarely superficially glutinous veil, subannulate; chrysocystidia not always present; spores large, often enormously

\*According to Kreisel (1979), *S. aeruginosa* sensu str. is merely one species of a group with blue to green pileus (*S. aeruginosus*, *S. ochrocyanea* Bon = *S. albocyanea* (Desm.) Quél., *S. caerulea* Kreisel and *S. squamulosa* (Mass.) Mass.); see also *S. aeruginosa* var. *neuquensis* Moser & Sing. and *S. albocyanea* var. *procera* Kreisel. - On the other hand, *S. aquamarina* Pegler is clearly a *Psilocybe*, and only externally similar to the stirps *Aeruginosa*, not related.

large; odor usually farinaceous. On dung and on manured fields and pastures and meadows.

Type species: *S. semiglobata* (Batsch ex Fr.) Quél.

*S. semiglobata* (Batsch ex Fr.) Quél.; *S. stercoraria* (Bull. ex Fr.) Quél.; *S. luteonitens* (Fr.) Quél. (*S. umbonatescens* (Peck) Sacc. sensu Kühner & Romagnesi), obviously also *S. bicolor* Pegler.

## 159. NAEMATOLOMA Karst.

Hattsv., Bidr. Finl. Nat. Folk 32: xxv. 1879.\*

Type species: *N. sublateritium* (Fr.) Karst.

**Characters:** Pileus non-hygrophanous or slightly hygrophanous in the marginal portion, usually with rather bright (yellow, fulvous, olive-yellow, purple) colors, not viscid, rarely viscid, usually with a thin, appendiculate veil; epicutis consisting of thin, hyaline, filamentous repent hyphae with clamp connections, sometimes gelatinized; hypodermium subcellular (distinctly so in most species); lamellae adnexed, adnate, or with decurrent tooth, neither deeply decurrent nor free; cystidia present in the form of chrysocystidia except in one section (*Stropholoma*) but then the hypodermium strongly subcellular; hymenophoral trama regular, consisting of parallel hyphal cells which are filamentous but mostly more or less inflated (though remaining parallel in the mediostratum; spore print as in *Stropharia*, more rarely a deeper duller brown ("cocoa" to "clove", M & P) (but then the hypodermium strongly subcellular and the stipe never glutinous or viscid); stipe centrally attached, relatively long, sometimes radicant, usually exannulate, rarely with a narrow annulus or with a broad white, membranous annulus, somewhat fibrous and rather tough in many species, usually becoming hollow at least in age often becoming brownish or deep fulvous from the base upwards, often fascicular-cespitoso; context often bitter, sometimes with abundant intercellular yellow pigment. On dead and living or buried wood, but also in deep moss (*Polytrichum*, *Bryaceae*, *Sphagnum*), often on *Carex* in swampy places, or on the forest soil or among needles, on charcoal, sticks, and in ruderal places.

In *Naematoloma* a marked tendency to form sterile populations is observed.

**Development of the carpophores:** Bivelangiocarpous or paravelangiocarpous, i.e. somewhat monovelangiocarpous in *N. polytrichi*).

**Area:** Cosmopolitan (or almost).

\*The transcription of νημα as naema is perfectly defendable for phonetic reasons even though not recommended. As long as the actual sequence of publications of *Hattsvampar* p. xxv and *Medd. Soc. Fauna Flora Fenn.*, p. 5, 1879 has not been established, there is no valid reason for changing the spelling to *Nematoloma* as has been done by most authors of the French school, inasmuch as Karsten in 1882 again used the spelling *Naematoloma* in his index. Some authors prefer to call this genus *Hypholoma* which is nomenclatorially untenable. If *Hypholoma* is used at all, it would replace *Psathyrella* rather than *Naematoloma* (see under *Psathyrella*) unless it is conserved by some future congress, with *H. fasciculare* or *H. sublateritium* as type species (by decree).

**Limits:** The distinction of *Naematoloma* from the other genera of the Stropharioideae is not difficult if the key characters are carefully considered. The position of section *Stropholoma* is intermediate between *Stropharia* (having the annulus), *Naematoloma* (having the hypodermial structure and scarcely hygrophanous pileus of that genus) and *Psilocybe* (having few or no chrysocystidia). The best solution appears to be its admission in *Naematoloma*.

On the other hand, the distinction between *Naematoloma* and *Pholiota* is at times difficult. While in the (typical) section *Naematoloma* the spore print is near "blue fox" or 8-H-3 (so in *N. fasciculare*), it tends to have a color intermediate between that of the Stropharioideae and the Pholiotoideae in some species such as *N. elongatipes* ("clove" M & P). The spore print alone cannot by itself be decisive in all cases, and it must be admitted that, here again, only the affinities of the species concerned can lead to a natural classification. If *Naematoloma* were limited to the species which have a lilac-livid spore color when the spores are studied fresh in water, it would be impossible to keep closely allied species together in a single genus. *N. elongatipes* is very close to *N. polytrichi* and *N. dispersum*, but differs from comparable Pholiotas in the absence of an annular veil (sect. *Albivelati*) and non-viscid pileus and stipe. It is closely related to *N. olymopianum* (A.H. Smith) A.H. Smith which, having essentially similar characters approaches *Naematoloma* even more closely because of its bitter taste and pseudorrhiza. It is the only Stropharioideae species known to us which has somewhat marbled spores and besides differs from *Pholiota* section *Subsiccae* by its non-gelatinized epicutis and the often truncate germ pore of the decidedly darker spores which are larger than those of that group of *Pholiota*. Other similar Pholiotas have glutinous stipe. Unfortunately, the type of development is unknown for *N. leongatipes*. If it were monovelangiocarpous or paravelangiocarpous it would probably be different from that of the Pholiotas of sect. *Subsiccae*. But at any rate, I believe, as do all authors except Smith & Hesler, that *Naematoloma elongatipes* is a *Naematoloma* rather than a *Pholiota* and that it differs from the nearest group in *Pholiota* by the characters indicated above.

Those species with glutinous stipe, even if they have an ambiguous spore print color like *N. mysosotis* are all in *Pholiota* where they form a subgenus (*Phaeonaemato-loma*) of mutually related species. Thus, the stipe in *Naematoloma* is always dry.

**State of knowledge:** With this definition, *Naematoloma* now contains 23 species. In spite of Kühner's (1936) valuable papers on European, A.H. Smith's (1951) monograph of North American, and my own descriptive data on South American species, a world monograph would still be desirable not only in order to register the still non-revised species and new forms but in order to untangle the remaining linnaeons (like *N. sublateritium*, *N. elongatipes*) which appear to cover more than one species or race.

**Practical importance:** *N. fasciculare* and other species growing on wood are occasional wood destroyers and may even contribute to the death of trees in the forests and plantations. Some species such as *N. sublateritium* are frequently used for food, especially in Italy, but require a special preparation. *N. fasciculare* has been reported to be poisonous (in Italy: M. Mortara & L. Martinello, 1955; Japan: D.

Narita, 1957; U.S.S.R.: Vasilkov, 1961). The same species contains a bacteriostatic substance (E.P. Silva, *Bol. Soc. Bot. Mex.* 24: 1-59. 1959). Other biologically active substances called naematoxin (Y. Ito, H. Kurita, T. Yamaguchi, M. Sato & T. Okuda, *Chem. Pharm. Bull.* 15: 2009-2010. 1967), muscarine and epimuscarine (Stadelmann et al. (*Helv. Ch. Acta* 59: 24-34. 1967), and fasciculol D (Kuda et al., *Agric. Biol. Chem.* 41: 1543-5. 1977) have been isolated from the same species. Undoubtedly, *N. popperianum* contains a biologically active alkaloid of the psilocybin group.

## SPECIES

Sect. 1. *CYANOLOMA* Sing. (1972). Spores medium sized (up to 12  $\mu\text{m}$ ); annulus well developed; chrysocystidia numerous; epicutis gelatinized; context and surfaces staining blue. On the soil in ruderal places and margins of the woods.

Type and only known species: *N. popperianum* Sing.

Sect. 2. *STROPHOLOMA* Sing. (1948). Spores medium or larger (often larger than 10  $\mu\text{m}$ ); annulus developed; on the forest soil, on fallen seeds, twigs, sticks, and logs; chrysocystidia moderately numerous to very scanty or absent (in the type species found absent).

Type species: *N. squamosum* (Pers. ex Fr.) Sing.

*N. squamosum* (Pers. ex Fr.) Sing.; *N. magnivelaris* (Peck) Sing.\*; *N. aurantiacum* (Cooke) Guzmán ex Sing.\*\*

Sect. 3. *NAEMATOLOMA* (*Flammuloides* Quél. 1886 ut sect. *Dryophilae*; *Cespitosa* Konr. & Maubl. 1948 ut sect. *Hypholomatis*; *Fascicularia* A.H. Smith 1951). Spores small (well below 10  $\mu\text{m}$ ); veil typically appendiculate only, absent in *N. nudum*, annulus inconstant, rarely developed, and if so developed, carpophores sometimes thick and large, sometimes smaller and thin, and usually growing in dense fascicles on wood.

Type species: *N. sublateritium* (Fr.) Karst.

*N. elaeodes* (Fr.) Konr. & Maubl. (*Hypholoma*, Gillet); *N. sublateritium* (Fr.) Karst. [*Hypholoma*, Quél.]; *Agaricus lateritius* Schaeff. ex Fr. non Batt. ex Fr.; *Hypholoma perplexum* (Peck) Sacc.]; *N. capnoides* (Fr.) Karst. (*Hypholoma*, Kummer); *N. epixanthum* (Fr.) Karst. (*Hypholoma*, Quél.); *N. radicosum* (Lange) Konr. & Maubl. (*Hypholoma*, Lange); *N. fasciculare* (Hudson ex Fr.) Karst. (*Hypholoma papillatum* Pat.; *Hypholoma flavovirens* Murr.); *N. clusiicola* Sing.; *N. castilloi* Sing.; *N. trinitense* (Dennis) Sing.\*\*\* (*N. amazonicum* Sing.); *N. nudum*

\*c.n. (*Stropharia magnivelaris* Peck in Harrim., *Alaska Exped.* 5 (*Crypt.*), p. 44. 1904). Orton (1960) considers that *A. percevalii* B. & Br. is identical and has priority, but lamellae-spacing and habitat are very different.

\*\*c.n. (*A. squamosus* var. *thraustus* f. *aurantiacus*, Cooke, *Handb. Brit. Fung.* 2nd ed. p. 199. 1883 with reference to *Ill.* 4: 555 [561]. 1884-1886. The combination "*N. aurantiaca* (Cooke) Guzman", *Nov. Hedw., Beih.* 51: 114. 1975 is invalid (Art. 33,2).

\*\*\*c.n. (*Pholiota trinitensis* Dennis, *Kew Bull., add. ser.* 3: 467. 1970).

Sing.; apparently also *Hypholoma aporum* Pegler (which shares its nontruncate spores with *N. amazonicum*).

Sect. 4. *PSILOCYBOIDES* Sing. (1948) [*Hypholoma* sect. *Tenuior(i)a* Konr. & Maubl. 1948; *Naematoloma* sect. *Tenacia* A.H. Smith 1951]. Spores often larger than 10 µm; annulus none, or rarely inconstantly and weakly developed; stipe usually rather thin, flexuous, and elongate; carpophores usually solitary or gregarious, not (or exceptionally) subfasciculate; on sticks, more often in deep moss, especially *Polytrichum* and *Sphagnum*, in marshy prairies and in humid forests, on sawdust, also in the subalpine shrub vegetation, in trundras and peat swamps; chrysocystidia constantly present.

Type species: *N. dispersum* Karst.

*N. dispersum* Karst. [*Hypholoma dispersum* (Fr.) Quél.; *Agaricus dispersus* Fr. 1838 non Pers. 1828; *Hypholoma marginatum* (Fr.) Schröter in Cohn; *Psilocybe ochraeiceps* Kauffm.]; *N. udum* (Pers. ex Fr.) Karst. (*Hypholoma* Quél.; *Psilocybe*, Gillet); *N. polytrichi* (Fr.) Konrad (sensu Ricken) [*Psilocybe uda* var. *polytrichi* Gillet; *Naematoloma* Karst.; *Hypholoma polytrichi* (Fr.) Ricken]; *N. elongatipes* (Peck) Sing. [*Psilocybe*, Sacc.; *Hypholoma*, A.H. Smith; ?*Agaricus elongatus* Pers. 1798 (pileus and lamellae green!), non *A. elongatus* Secr.; *Naematoloma elongatum* ("Pers." ex Secr.) Konrad (sensu Konrad); *Galerula paludicola* Atk.]; *N. ericaeum* (Pers. ex Fr.) Sing. (sensu Kühner (*Psilocybe*, Quél.); *N. subumbonatescens* (Murr.) Sing. (*Stropharia*, Murr.) unless too close to the proceeding species; *N. subericaceum* (Fr.) Sing. (*Psilocybe*, Sacc.; *Hypholoma*, Kühner); *N. puiggarii* (Speg.) Sing.

## 160. *PSILOCYBE* Kummer

Führ. Pilzk. p. 21. 1871.

Type species: *Agaricus montanus* Pers. ex Fr.

Syn.: *Psilocybe* (Fr.) Quél., Champ. Jura Vosq. p. 147, 1872-3, non Fayod 1889.

*Deconica* (W.G. Smith) Karst., Bidr. Finl. Nat. Folk 32: xxvi. 1879.

*Pholiotella* Speg., Bol. Acad. Cienc. Cordoba 11: 412. 1889.

*Delitescor* Earle, Bull. N. Y. Bot. Gard. 5: 434. 1909.

*Galeropsina* Velen., Nov. Myc. Noviss. p. 74. 1947, with the type species: *G. pyrispora* Velen.\*

Characters: Pileus cylindric-conic or semiglobate to convex, campanulate, often umbonate or papillate, subviscid, or viscid, or hygrophanous, or dry; epicutis consisting of thin, hyaline, filamentous, repent, not to rather strongly gelatinized, thin-walled, clamped hyphae; hypodermium consisting of hyphae somewhat broader than those of the epicutis, even considerably inflated, but generally forming a cutis and not subcellular but strictly radially arranged; veil varying from annular to almost nil, often floccose on pileus and stipe, mostly fugacious, in few species per-

\*"gen. et sp. nov." is accepted as meaning that the description of *G. pyrispora* is a descriptio generico-specifica even though a second species is indicated but apparently with some doubt and in disagreement with the first description. If not admitted under Art. 42.1, the genus is not validly published according to Art. 41.2. *G. pyrispora*, type, is a *Psilocybe* (PR).

sistently annulate; lamellae narrow to much more frequently broad, even extremely broad, adnexed to adnate, often with decurrent tooth; cheilocystidia constantly present; cystidia present or absent, but never in form of chrysocystidia excepting in a few species which are strictly exannulate, hygrophanous, and with non-subcellular, exceptionally slightly subcellular hypodermium; hymenophoral trama regular but its hyphae tending to become soon interwoven and irregular in size of the hyphal cells; spore print deep lilac to fuscous-sepia or purplish brown; spores with complex wall but smooth, without ornamentation, small to large, often lentiform (clearly narrower in lateral than in frontal view), with truncate germ pore, in KOH melleous-brown to olive or deep chestnut, in water when fresh either lilac-livid or melleous-ochraceous to ochraceous-brown (Pl. 13); stipe not viscid, central, glabrous or with fibrillose coating, or flocculose from the veil, rather long to very long and not curved but at times somewhat flexuous, usually narrowly hollow, sometimes radicant (but then without chrysocystidia), context sometimes bluing (or surfaces bluing when touched or bruised), odor raphanaceous or farinaceous, not astringent—"bitter" and aromatic as in *Naematoloma fasciculare*; all hyphae with clamp connections; pigment mostly intraparietal and often incrusting. On sticks, stems, branches, culms, leaves and other litter, also among moss, on earth, on seeds, frequently on dung, sawdust, straw, bagasse, dead woody material (logs, Pteridophyta, Mono- and Dicotyledones).

*Development of the carpophores:* Bivelangiocarpous (so in *P. merdaria*, *P. coprophila*, *P. cubensis*, *P. cробulus*) or monovelangiocarpous (in *P. mexicana*, *P. semiperviva*, *P. zapotecorum*) as interpreted by Reijnders; hymenocarpous or pileostipitocarpous (Reijnders). Under certain conditions, especially when grown in conditions of insufficient light, carpophoroids ("sclerotia") are formed instead of normal carpophores in some species, particularly in *Psilocybe mexicana*, *P. sierrae*, *P. sclerotifera*.

*Area:* Almost or quite cosmopolitan.

*Limits:* The genus is easily circumscribed among the Stropharioideae. As in other genera of this subfamily it is at times more difficult to decide whether a species belongs to *Psilocybe* or some genus of the Pholiotoideae.

The genus *Psilocybe* differs from *Pholiota* principally in the color of the spore print. However, there are cases where the spores are similarly colored in certain groups of both genera, and in this case it should be remembered that the species of *Psilocybe* with chrysocystidia (sect. *Chrysocystidiatae*) differ from section *Subsiccae* of *Pholiota* - the only comparable one - in truncate germ pore of the mostly lentiform spores, more hygrophanous (sometimes under a velar layer) pileus, absence of a gelatinized hymenopodium, and the typical habit of the smaller *Psilocybes*. The species without cystidia differ from *Pholiota* subgenus *Hemipholiota*, *Pholiota* sect. *Flavidula*, and subgenus *Flammula* sect. *Flammula* by approximately the same characters as far as section *Psilocybe* and *Atrobrunneae* are concerned, and by the spore color, combined with broad germ pore as far as the other sections are concerned. It should also be noted that species growing on dung or bluing by autoxidation are generally *Psilocybe* rather than *Pholiota*. The only case where an actual

confusion of the two genera has taken place is that of *P. septembris* which, because of the color of the spores in KOH (rusty ochraceous brown) had been erroneously described in *Pholiota* where it would be comparable only with the stirps *Spumosa* from which it differs by the much deeper colored spores with a broad truncate germ pore and the habit (relatively long, thin stipe, extremely broad lamellae) and absence of yellow pigment.

*Psilocybe* is also close to *Kuehneromyces*. EM data on spore ornamentation are available (Cléménçon; Pegler & Young, Oláh) for *K. mutabilis* (spores ornamented) and *P. bullacea* and *quebecensis* (spores smooth) which, if generalized would provide a sharp limitation. Otherwise we depend on spore print color which is generally sufficiently different in these genera. In a case like *K. depauperata* where a good spore print has not yet been obtained, it is quite possible that Smith & Hesler (1968) are right suspecting that this species belongs to *Psilocybe* rather than *Kuehneromyces*.

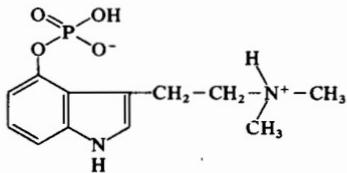
Some authors, including authors of very recent works, have considered *Deconica* as an autonomous genus. Up until very recently, and including the period of 1941-51 when the first edition of the present work was edited, it appeared to this author that these genera are separable on the basis of a character which is very easy to observe, viz. the shape and size of the spores. This character is correlated with at least one other character as far as the species then known to us were concerned. Thus, the hygrophanous pileus of many Deconicas, the pleurocystidia of many Psilocybes served as additional indication in the delimitation of these genera from each other.

However, in recent studies on extra-European material, particularly from the Western Hemisphere, the delimitation has become rather difficult because of a small number of forms which have small non-lentiform or large lentiform spores or combine "Deconica"-spores with other characters not found in typical European Deconicas. To this evidence is added the experience gained in the monographic work on sect. *Caerulescentes* by Singer & Smith ("teonanácatl") where we found that both habits, the typical *Deconica*-habit and the habit of *P. semilanceata*, can be observed in very closely related species, and that there are species with lentiform, less lentiform and non-lentiform spores in the same undoubtedly natural group. Furthermore, it was possible on the basis of exclusively European material to postulate that *Deconica* does not have pleurocystidia. In tropical and American material, species with cystidia, and at the same time lentiform spores and "Deconica-habit" have become known (e.gr. *P. alnetorum*). This tends to weaken the hiatus between *Psilocybe* and *Deconica* even further. Consequently, I cannot see that *Deconica* can be maintained as an independent genus. The section 7 (*Chrysocystidiatae*) is so closely allied to sect. 6. (*Psilocybe*) that the exclusion of the species with chrysocystidia - relegating them to *Naematoloma* or *Pholiota* is extremely artificial. All Strophariaceae with wholly and distinctly hygrophanous pileus and the habit of *Deconica* (i.e. sect. *Psilocybe*), with small pore-bearing spores and lacking a membranous or glutinous veil are inseparable from *Psilocybe*.

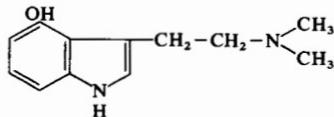
*State of knowledge:* Until recently, only one section had been worked out monographically, viz. sect. *Caerulescentes*. The other sections including *Caerulescentes*

but excluding *Chrysocystidiatae* were monographed by Guzmán (1983) who treats 144 species. We enumerate 67 species below.

*Practical importance:* Several species of the sect. *Caerulescentes* are used by the Indians of Mexico and Guatemala as a drug. This use\* originated in pre-Colombian times and was at that time - and occasionally still is - used in a religious rite. The fact that at least one species of this group is used as a drug in Mexico was first pointed out by this author in the first edition of the present work (1951). Studies carried out between 1957 and 1960 by Heim, Singer, V.P. and R.G. Wasson, have shown that the species concerned are of great ethnological and - what is more important - physiological and medicinal interest since the hallucinogenic principle involved appears to act as an antimetabolite for serotonin in the human brain. One of the hallucinogenic substances isolated by a group of chemists of the Sandoz Laboratory in Basel, Switzerland, is psilocybin with the formula:



A derivative substance occurring together with psilocybin is psilocin:



It is to be expected that some species contain additional hallucinogenic substances, or replace psilocybin and psilocin by still unknown compounds (cf. Hofmann et al., *Experientia* 14: 397-401. 1958; 15: 101-104. 1959).

The hallucinogenic, or psychotropic, as well as the poisonous *Psilocybes* are of great interest in neuropsychiatric research and their action upon the human brain as well as the action of the substances isolated from them have strongly influenced psychiatric research and practice, as have fungi with known psychotropic activity.

In the same group, there are also poisonous species which when eaten are sometimes deadly. One of these is *P. argenteipes* Yokoyama, another *P. aeruginosumaculans* or *P. subaeruginascens* (both apparently determined as *Stropharia* or *Psilocybe venenata* in Japan).

As had been pointed out by Singer & Smith (*Mycopathologia et Mycl. Appl.* 9: 281. 1958) and later confirmed by biochemical work, a relation between the bluing of the carpophores of this type of Agaricales (Coprinaceae, Bolbitiaceae, Strophariaceae, Cortinariaceae) and the capacity to provoke cerebral mycetism exists. Thus the oc-

\*See also Singer in Rumack & Salzmann, *Mushroom Poisonings: Diagnosis and Treatment* p. 202-207. CRC Press, Inc. 1978.

currence of psychotropic alkaloids and the oxidative transformation of these, resulting in blue pigments, must be linked. This rule led to the discovery of psilocybin and related substances in other bluing species as predicted by us: *Psilocybe cyanescens*, *baeocystis*, *pelliculosa*, *semperviva*, *cubensis*, *cookei*, *Pholiota cyanopoda*, *Gymnopilus purpuratus*, *Panaeolus subbalteatus*, *Copelandia chlorocystis*, *C. cyanescens* and *Inocybe aeruginascens*. According to Tyler, psilocybin is converted to psilocin by mammalian tissue homogenates and the latter compound is subsequently changed to a blue product by oxidation, possibly an o-quinone derivative. Psilocin occurrence is thus not limited to *Psilocybe*, but occurs throughout the families with binucleate, pigmented spores.

## SPECIES

Sect. 1. *MERDARIAE* (Fr.) Sing. Pileus neither acute nor conic-campanulate; veil often strongly developed, even annular; cystidia on the sides of the lamellae present or absent; spores larger than 9  $\mu\text{m}$  and in some species up to 20.3  $\mu\text{m}$  long; context not bluing; spores not lenticular, or slightly lenticular and then often subangular and rather large. On dung, on manured fields and pastures, on beds, also in sand dunes, and in high-andine *Stipa* associations, rarely on carpophores of Basidiomycetes.

Type species: *P. merdaria* (Fr.) Ricken.

*P. merdaria* (Fr.) Ricken; *P. merdicola* Huijsman; *P. anellariiformis* (Murr.) Sing.; *P. subcoprophila* (Britz.) Sacc.; *P. argentina* (Speg.) Sing.; *P. mesospora* Sing.; *P. praetervisa* Sing.; *P. coprophila* (Bull. ex Fr.) Kummer; *P. dunicola* (Speg.) Sing.; *P. squarrosipes* Sing.; *P. blattariopsis* (Speg.) Sing.; probably here *P. longinqua* Sing. and *P. fuegiana* (Horak) Sing. - According to Guzmán (1983) part of this section is transferred to *Atrobrunneae* and *P. dunicola* and *P. squarrosipes* are considered synonyms of *P. sabulosa* Peck. I find this synonymy doubtful, and the separation of non-hexagonal and hexagonal-spored species in different sections unjustified (because it takes *P. coprophila*\* and *P. subcoprophila* into different sections) and difficult (because both spore shapes are often found in a single spore print).

Sect. 2. *CAERULESCENTES* Sing. (1948)\*\*. Habit very variable; annulus absent or present and fugacious or persistent; spore size variable and spores lenticular or not; context bluing on exposure and/or surfaces bluing ("deep Medici blue" Ridgway) when touched or scratched, strongly reacting with monomethylparamido-phenol, rarely only the veil becoming bluish.

Type species: *P. cubensis* (Earle) Sing.

Stirps Cubensis. (Annulus distinct and rather persistent or if fugacious, carpophoroids ("sclerotia") present).

\*In the index (p. 421) *P. coprophila* is placed (erroneously?) in sect. *Cordispora[e]*.

\*\*Sect. *Cubensae* (sic) Guzmán (1983, p. 245) based on the type species of sect. *Caerulescentes* is a superfluous name. The same author has placed other species of bluing Psilocybes in other sections which are mostly on the same level as our (Smith & Singer 1958) stirpes; some of these might be recognized as sub-sections or series.

*P. cubensis* (Earle) Sing. (*P. subcubensis* Guzmán); *P. subaeruginascens* Höhnel; *P. aerugineomaculans* Höhnel; obviously also *P. venenata* Imai (which seems to be identical with either one of the two preceding species); *P. caesioannulata* Sing.; *P. fimetaria* (Orton) Watling; *P. caeruleoannulata* Sing. ex Guzmán; *P. uruguayensis* Sing. ex Guzmán; *P. sierrae* Sing. (SGO. as *P. maulensis* in sched.); apparently also *P. sclerotifera* (Speg.) Sing. and *Stropharia aquamarina* Pegler.

Stirps Yungensis. (Spores small, up to 7.7  $\mu\text{m}$  long, strongly lentiform; pileus acute or with appendage; stipe thin; on forest litter and wood).

*P. yungensis* Sing.; *P. isauri* Sing. (= *P. yungensis* acc. to Guzmán); *P. hoogshagenii* Heim; *P. dumontii* Sing. ex Guzmán.

Stirps Mexicana. (Spores medium sized; otherwise like the preceding stirps; habit mycenoid with young margin straight or almost so; producing carpophoroids; in open places on earth).

*P. mexicana* Heim.

Stirps Silvatica. (As preceding stirps but spores not lentiform, often larger; carpophoroids unknown; mostly not in habitats outside the forest.)

*P. silvatica* (Peck) Sing. & Smith; *P. pelliculosa* (A.H. Smith) Sing. & Smith; *P. cookei* Sing.\*

Stirps Cyanescens. (Spores typically more than 9  $\mu\text{m}$  long; annulus none; veil otherwise well developed, at times subannuliform but fugacious, or slight; habit collybioid or nearly so; on earth and on rotten wood.)

*P. aztecorum* Heim; *P. cyanescens* Wakefield; *P. baeocystis* Sing. & Smith; *P. strictipes* Sing. & Smith; *P. araucana* Sing.; *P. collybioides* Sing. & Sm.; *P. mairei* Sing. (*Hypoloma cyanescens* Maire non *P. cyanescens* Wakefield); obviously also *P. fasciata* Hongo\*\* and *P. serbica* Moser & Horak (unless too close to *P. mairei*).

Stirps Caerulescens. (As preceding stirps but spores smaller).

*P. caerulescens* Murr. (*P. mazatecorum* Heim); *P. aggericola* Sing. & Smith; *P. can-didipes* Sing. & Smith; *P. boliviarii* Guzmán; *P. zapotecorum* Heim.

Stirps Caerulipes. (Differing from stirps Caerulescens in smaller size and thinner stipe: 1-3 mm at apex; spores  $< 10 \mu\text{m}$ ).

*P. muliercula* Sing. & Smith (*P. wassonii* Heim\*\*\*); *P. caerulipes* (Peck) Sacc.; *P. argentipes* Yokoyama.

\* “*P. cookei* Sacc.” as quoted by Guzmán (1983) was published as a variety of *P. sardocephala* and was thus understood by Rea (and Orton), long before Killermann (1936). It is not homonymous with *P. cookei* Sing. and the latter not conspecific with *P. callosa* which is a non-bluing species of sect. *Tenaces*.

\*\* *P. fasciata* is thought to be identical with *P. venenata* Imai (Guzmán 1983).

\*\*\* In “A Correction” (*Ethnomy. Stud., Harvard Un.* 8: 1-6. 1982) I quoted (p. 3) Heim’s 1957 paper as *C.R. Acad. Sc.* 242. 1393 which obviously should have been *C.R. Acad. Sc.* 245: 1761-[1765]. 1957] inasmuch as vol. 242 was published 1956. Wasson (*Bot. Mus. Harvard Un.* 8: 1-3) who knew perfectly well that the erroneous citation referred to a paper published earlier than the one that contained a phrase hinting at Heim’s intention to publish a *P. wassonii*, nevertheless exploited this error as supposedly

R. Heim (1959, 1967) mentions also as belonging to the same section the following species: *P. cordispora* Heim, *P. acutissima* Heim, *P. mixaensis* Heim, *P. kumaenorum* Heim, and *P. quebecensis* Oláh & Heim - species which I have not analyzed myself.

Sect. 3. *TENACES* (Fr.) Sacc. (1887). (*Semilanceatae* Guzmán 1983). Differing from the preceding section in not bluing; pileus cylindric-fusoid-acute or convex becoming applanate, slightly viscid and weakly hygrophanous or hygrophanous only in the marginal zone, color of the pileus often with fulvous ochraceous or olive tinge; veil little developed, but leaving an appendiculate veil remnant on the margin of the pileus in some cases, generally not membranous but mostly fibrillose-cortinoid, never annulate; spores  $>8.5 \mu\text{m}$ , mostly  $>12 \mu\text{m}$ , not lenticular; cheilocystidia generally small, up to  $38 \mu\text{m}$  long; pleurocystidia mostly none, or scarce, or in form of cystidioles (differing from *Naematoloma* sect. *Psilocybooides* which is often similar in habit, in the absence of chrysocystidia); habit in mud of swamps, in mossy ditches in shaded places, on peat, sticks, decayed trunks, also on earth in low clearings, margins of the woods and in open coniferous woods, on burned ground, not on dung; temperate species only.

Type species: *P. semilanceata* (Fr. ex Secr.) Kummer.

*P. semilanceata* (Fr. ex Secr.) Kummer\*; *P. paupera* Sing.; *P. callosa* (Fr. ex Fr.) Quél.; *P. carbonaria* Sing. - *P. flammuliformis* Sing., tentatively placed here, is of dubious affinities (a spore print is wanting) but the spores in KOH are differently colored than in *Pholiota* sect. *Flammula* which is otherwise similar as pointed out by Guzmán (1983).

Sect. 4. *ATROBRUNNEAE* Sing. (1948). Pileus campanulate to convex or conic at first, hygrophanous; stipe with fibrillose-velutinous coating or sometimes glabrous, exannulate, generally elongate; veil little developed and always absent in mature specimens; pleurocystidia few or none, often inconspicuous; on mud in swamps, among *Sphagnum*, also on other mosses over small sticks, on needles, on earth, or on peat, never on dung; not bluing; odor and taste often farinaceous, raphanaceous, or acrid. Temperate species.

Type species: *P. atrobrunnea* (Lasch) Gillet.

*P. atrobrunnea* (Lasch) Gillet (*P. dichroa* Karst.; *P. fuscofulva* Peck; *P. turficola* Favre - synonymy according to A.H. Smith), the type (sensu Lasch) which I recollect has raphanaceous odor and slightly hexagonal sublentiform spores (LE). - Here possibly also *P. fuegiana* (Horak) Sing. sensu Sing.

showing that I had indeed knowledge of Heim's intentions when we described *Psilocybe muliercula*, and thus justifying Ott's argument which had caused the whole controversy. The ethics involved in Wasson's paper are lamentable and unworthy of a person who pretends, in the same paper, to have a "responsibility to history".

\*This is a non-bluing species as described and as often observed in Europe and South America. A similar bluing species (*P. semilanceata* sensu Heim, Guzmán; var. *caeruleescens* Cooke) is *P. cookei* Sing. (sect. *Caerulescentes*).

Sect. 5. *SEPTEMBRES* Sing. (1972). Spores smaller than in most species of section 3 and 4, not livid or lilac when fresh in water mounts, up to 10.5  $\mu\text{m}$  long; differs from the two following sections in conspicuous pleurocystidia which are neither in shape nor in contents like the chrysocystidia; veil often annulate or surface of the stipe shiny; not bluing. Neither growing on sand dunes nor on *Sphagnum* nor on charcoal. Species of the southern Hemisphere, one north-temperate.

Type species: *P. septembris* (Sing.) Sing.

*P. septembris* (Sing.) Sing. (*Pholiota septembris* Sing.); *P. marthae* Sing.; here also a species from Jujuy erroneously (but validly) published under the name *P. cordobensis* Sing.; obviously also *P. bulbosa* (Peck) A.H. Smith.

Sect. 6. *PSILOCYBE* (*Agaricus* subg. *Deconica* W.G. Smith; sect. *Deconica* (W.G. Smith) Sing.). Pileus not campanulate or conic but convex to hemispherical, sometimes with a small umbo or papilla, or quite obtuse, hygrophanous, becoming much paler when faded, with or without some velar floccos or a slight silky velar zone at the margin, generally not annulate, rarely fugaciously subannulate; epicutis gelatinized or not; lamellae horizontal, broad, broadly adnate, often with decurrent tooth; cheilocystidia numerous, but cystidia absent on the sides of the lamellae; spores generally small (rarely reaching as much as 11  $\mu\text{m}$ ), 0.5-1.3  $\mu\text{m}$  broader when seen frontally than in lateral view, i.e. lentiform, often heart-shaped or rhombic when seen frontally, either lilac to livid or melleous- to brownish ochraceous when seen fresh in water mounts (Pl. 13); stipe central, with or without traces of the veil but rarely with an apical fibrillose line or zone, pigmented inside at least towards the base. On fallen leaves and stems, mosses, dead wood, straw, dung, peat etc. Not bluing.

Type species: *Psilocybe montana* (Pers. ex Fr.) Kummer.

*P. montana* (Pers. ex Fr.) Kummer (*Psilocybe atrorufa* (Schaeff. ex Fr.) Quél.); *P. muscorum* (Orton) Moser in Gams; *P. heterosticha* (Fr.) Sing. (*A. furfuraceus* var. *heterostichus* Fr. sensu Sing. 1931); *P. omniumsanctorum* Sing.; *P. valdiviensis* Sing.; *P. velifera* (Favre) Sing.\*; *P. crobula* (Fr.) Morton Lange ex Sing.; *P. angulata* (Batsch ex Pers.) Sing.; *P. ecbola* (Fr.) Sing. (*P. inquilina* (Fr. ex Fr.) Bres. sensu Lange); *P. physaloides* (Bull. ex Mérat) Quél. (sensu Fr. non Bres.); *P. rhombispora* (Britz.) Sacc.; *P. pteridophytorum* Sing.; *P. palmigena* (Berk. & Curt.) Sacc. (*Deconica*, Sing.); *Psilocybe* "cf. *modesta* (Peck) Smith" Dennis, *Fung. Fl. Venez.* p. 70. 1970); *P. bullacea* (Bull. ex Fr.) Kummer (sensu Ricken); *P. subviscida* (Peck) Kauffm. (*Deconica graminicola* Orton); *P. xeroderma* Huijsman (*Geophilus hyperella* (Fr.) Kühner & Romagnesi sensu Kühner & Romagnesi); *P. subhyperella* Sing.; *P. albofimbriata* (Rick.) Sing.\*\*

Sect. 7. *CHYSOCYSTIDIATAE* Sing. (1972). Differs from sect. 6 only in the

\*c.n. (*Geophilus velifera* Favre, *Rés. rech. sc. Parc Nat. Suisse* 5: 204. 1955).

\*\*c.n. (*Naucoria albofimbriata* Rick, *Iheringia* 8: 393. 1961). There is no indication that this species is bluing and its type has smaller spores than *P. farinosa* Rick ex Guzmán. If the two were identical they should be called *P. albofimbriata*.

presence of chrysocystidia on the sides of the lamellae; these sometimes without amorphous yellowish contents in KOH but in shape like chrysocystidia; spores sometimes scarcely or not lentiform. Differing from *Naematoloma* in hygrophanous pileus and shape of carpophores.

Type species: *P. chrysocystidiata* Sing.

*P. alnetorum* (Sing.) Sing.; *P. peruviana* Sing.; *P. chilensis* Sing.; *P. lazoi* Sing.\*; *P. chrysocystidiata* Sing.; *P. peladae* Sing.; *P. cokeriana* A.H. Smith; *P. aequatoriae* Sing., here also a species from Cordoba, Argentina, erroneously (but validly) described as *P. jujuyensis* Sing.; *P. goniospora* (Berk. & Br.) Sing.

## 161. MELANOTUS Pat.

*Esai tax.* p. 175. 1900.

Type species: *M. bambinus* Pat.

**Characters:** Pileus convex, hygrophanous or not, epicutis a cutis, ixocutis, or trichodermium, pigmented or not; stipe eccentric, mostly curved, relatively short to very short, spore print as in *Psilocybe*; spores relatively small, in some species up to 10.5 µm long, lentiform or not, with complex but homogenous smooth wall, with apical germ pore; context made up of hyphae with clamp connections, not gelatinized in the trama; on wood, débris, fabrics (Pl. 6).

**Development of the carpophores:** Unknown but probably "hemiangiocarpous"; details unknown.

**Area:** Most species limited to the subtropical and tropical regions, but at least three species in the north-temperate and a few species in the south-temperate zone; only three species occur in Europe.

**Limits:** The genus is obviously closest to *Psilocybe* from which it differs sharply in habit. The species of *Melanotus* have in the past often been confused with *Crepidotus*. It differs from that genus by its spores with germ pore. It may be confused with *Pleuroflammula* (see there), and *Pyrrhoglossum* (the latter with verrucose spores).

**State of knowledge:** 20 species are now recognized.

**Practical importance:** One species (probably *M. musaecola*) is an active destroyer of fabrics in the tropics (Pl. 5). It has been reported as such under the erroneous name *Claudopus variabilis* (*Mycologia* 38: 677. 1946). The fungus has been seen by the author, and belongs undoubtedly in *Melanotus*.

## SPECIES

On wooden boards, trunks and stumps, tree bark, dead dicotyledonous branches.

\*Type at SGO, with cheilocystidia, not bluing. The NY "type" studied by Guzmán (1983, p. 270, 271) may be different.

*M. proteus* (Kalchbrenner) Sing. [Claudopus, (Kalchbr.) Sacc., on manufactured wood in South Africa]; *M. flavolivens* (Berk. & Curt.) Sing. [Crepidotus, (B. & C.) Sacc. on dead wood on Bonin Isls.]; *M. fumosifolius* (Murr.) Murr. (Crepidotus, Murr., on dead log on Jamaica, W.I.); *M. haematites* (Berk. & Curt.) Sing. [Crepidotus, (B. & C.) Sacc., on dead wood in Hong Kong]; *M. psychotriae* (Pat.) Sing. (Crepidotus, Pat., on *Psychotria glabrata*); *M. subvariabilis* (Speg.) Sing. (Claudopus, Speg., on "rotting branches" in Brazil); *M. hepatochrous* (Berk.) Sing. (Crepidotus, Sacc.); *M. gayi* (Pilát) Sing.; *M. patagonicus* Sing.; *M. polylepidis* Sing.; *M. brevisporus* Sing.; *M. poliocephalus* Sing., apparently also *M. hartii* Ammirati in Amm. et al. and *M. horizontalis* (Bull. ex St Amans) Orton sensu Orton.

On bamboo; leaves, culms and trash of Monocotyledones (*Musa*, *Zea*, *Carex*, *Juncus* etc., rarely on other herbaceous débris).

*M. bambinus* Pat.; *M. musaecola* (Berk. & Curt.) Murr.; *M. eccentricus* (Murr.) Sing.; *M. phillipsii* (Berk. & Br.) Sing.; *M. cassiaeicolor* (Berk.) Sing. (on both Mono- and Dicotyledones, mostly the former); *M. caricicola* (Orton) Guzmán.

On Pteridophyta:

*M. ridleyi* (Mass.) Sing.

On palms (decaying coconut husks and other palm débris):

*M. subcuneiformis* (Murr.) Sing.

#### Subfamily Pholiotoideae (Imai) Sing.

*Agar. mod. Tax.* 1st ed. p. 511. 1951.

Type genus: *Pholiota* (Fr.) Quél.

Syn.: *Pholiotoideae* Imai, *Journ. Fac. Agr. Hokk. Imp. Univ.* 43(2): 179. 1938 (ut subfam. Agaricacearum).

*Pholioteae* Fayod, *Ann. Sc. Nat. Bot.* VII. 9: 360. 1889 (ut tribus Pholiotés); Romagnesi, *Rev. Mycol.* 2: 23. 1937 (ut tribus Pholioteae); Imai, l.c. (ut tribus Pholioteae).

Characters: Same as in the family, but spore print more brown than in subfam. Stropharioideae, e.gr. between "tiffin" and "Antique bronze", "Antique gold", 15-E-12, "oak", also reaching "cochin" or between "Cochin" and "Sudan br.", "clove", "raw sienna", "Amber br.", "coffee" to "Malay", "cognac", between "kis kilim" and "cocoa", "bunny" to "bronze" M & P; - "snuffbrown", "Brussels brown", between "Verona brown" and "cinnamon brown", "Argus brown", between "Argus brown" and "Brussels brown", "Dresden brown", between "cinnamon rufous" and "hazel", more rarely brighter rusty (almost like *Conocybe tenera*) or "cinnamon-fulvous", reaching almost "sepia" - Ridgway; - 6-E-8 in Methuen Handbook of Color 1967; by dehydration either little changed, or if near "clove" (M & P) drying more yellowish brown; spores under the microscope never lilac or livid in water mounts if studied in fresh condition; context not bluing.

Limits: See under Stropharioideae and the genera of Pholiotoideae.

## KEY TO THE GENERA

- A. Habit pleurotoid or not; pleurocystidia none (no chrysocystidia either).
- B. Habit pleurotoid; hyphae of the epicutis neither very broad nor thick-walled nor incrusted by crystals or by coarse brown pigment. 165. *Pleuroflammula*, p. 589
- C. Epicutis not pleurotoid, or else epicutis consisting of elements which are broad (not filamentous) with firm to thick wall, with crystalline or coarse brown pigment incrustations.
- D. Epicutis distinctly gelatinized, - a pellicle, or else pileus rather large to very large and stipe correspondingly thick and broad (more than 4.5 mm broad), often white or whitish.
- E. Pileus only partly or weakly hygrophanous; stipe often white or whitish all over; margin of pileus not or very short (2 mm) transparently striate; pileus and stipe often large and fleshy (stipe in this case more than 4.5 mm broad); pileus scaly or not; spores with or without a truncate to non-truncate germ pore, often bean-shaped, sometimes large (see "H" below: *Pholiota*).
- F. Pileus strongly hygrophanous and margin of pileus transparently striate; stipe not white nor whitish all over; pileus and stipe rarely large and stipe not over 12 mm broad; pileus not scaly, but glabrous (but stipe may be squamose); spores with truncate germ pore, never bean-shaped, up to 11  $\mu\text{m}$  long (see "G" below: *Kuehneromyces*).
- D. Epicutis neither distinctly gelatinized nor pileus or stipe very large and fleshy, the latter not over 8 mm broad and not entirely white or whitish rarely whitish-pallid and then pileus without a pellicle and without scales.
- G. Spore print often rusty or very bright cinnamon-fulvous, or else spores under the microscope (in KOH) rufous-red-brown or richly ferruginous almost like *Conocybe*-spores, with a narrow to broad, truncate or non-truncate germ pore, with thick (about 0.7-1.7  $\mu\text{m}$ ) complex, smooth wall, 7-14  $\mu\text{m}$  long, ellipsoid to ovoid, mostly broad and often somewhat rounded-rhombic in frontal view; epicutis hygrophanous only if the pileus is squarrose and only then with a broadly transparently striate margin when wet, otherwise weakly hygrophanous (and then not transparently striate) or dry; on the earth in xerophytic vegetation or on charcoal or rotting wood in very humid conditions. 164. *Pachylepyrium*, p. 588
- G. Spore print and spores less bright colored ("oak", between "Cochin" and "Sudan br." M. & P., or even less bright in print, never bright rusty or rufous-red-brown in KOH), smooth under the light microscope, but verrucose under the EM (at least in the type species), not larger than 11  $\mu\text{m}$ , mostly smaller, typically with a broad truncate germ pore; pileus strongly hygrophanous, glabrous and naked, transparently striate on woody matter (trunks, chips, logs, sawdust), mesophytic, not on charcoal. 163. *Kuehneromyces*, p. 584
- C. Epicutis characteristically formed by broad, elongated or spherocyst-like elements, either in chains or becoming free (and then pileus pulverulent), always strongly incrusted by an incrusting ochraceous-brown or ferruginous-brown pigment or by a crystalline incrustation, forming a thin cutis-like or thick tomentose trichodermium; spores mostly without a germ pore, more rarely with a narrow, non-truncate one; spore print normally brown, or paler and more ochraceous (like "Nankeen" "spruce y.", "Inca gold" M. & P.); stipe central or more rarely eccentric. 166. *Phaeomarasmius*, p. 590
- A. Habit never pleurotoid; pleurocystidia or some sort (often chrysocystidia) present.
- H. Pileus hygrophanous, transparently striate; pleurocystidia like the cheilocystidia, not thick-walled; hymenopodium not gelatinized; spores not pseudoamyloid, with distinct germ pore (See "F" above). 162. *Pholiota*, p. 576
- H. Pileus or cystidia or hymenopodium or spores different.

Führ. Pilzk., p. 22. 1871, nom. cons. (as *Pholiota* (Fr.) Kummer\*).

Type species: *Pholiota squarrosa* (Pers. ex Fr.) Kummer.

Syn.: *Agaricus* trib. *Pholiota* Fr., Syst. Mycol. 1: 240. 1821.

*Agaricus* trib. *Flammula* Fr., l.c. p. 250.

*Pholiota* (Fr.) Quél., Champ. Jura Vosg. p. 124. 1872-3.

*Flammula* Kummer, Führ. Pilz. p. 22. 1871 non D.C.

*Flammula* (Fr.) Quél., Champ. Jura Vosg. p. 129. 1872-3, non D.C.\*\*

*Dryophila* Quél., Enchiridion, p. 66. 1886.

*Flammopsis* Fayod, Prodrôme, Ann. Sc. Nat. Bot. VII. 9: 356, 1889\*\*.

*Visculus* Earle, Bull. N. Y. Gard. 5: 437. 1909.

*Hypodendrum* Paulet ex Earle, l.c. p. 445.

*Nemecomyces* Pilát, Ann. Mycol. 31: 54. 1933\*\*\*.

**Characters:** Pileus squamose or naked or tomentose, viscid (with a gelatinized epicutis) or not, non-hygrophanous, or rarely hygrophanous (mostly only in part) and then not showing the ensemble of characters of *Kuehneromyces*, lamellae variously attached; hymenophoral trama regular; spore print frequently with rusty hue but not bright ferruginous as in *Conocybe*, usually argillaceous brown or ochraceous brown to tobacco brown, more rarely a deeper brown (like a deep chocolate brown, somewhere between "chocolate" and "Mandalay" or towards "clove" M. & P.) but then either spores *never* with a broad and truncate germ pore or stipe *with* a glutinous covering *or* hypodermium distinctly cutiform and epicutis not gelatinized; spores under the microscope in KOH neither rufous-red-brown, bright rust (like *Conocybe*), nor olive, and when fresh in water never lilac or livid, with or without a germ pore, smooth even in EM sections (at least in the species studied in this regard), always smooth under the light microscope, ochraceous to ochraceous brown or melleous in most when seen in ammonia; pleurocystidia present or absent, if present either thin-walled and optically "empty", or almost metuloid (with partially thickened wall), or chrysocystidioid, i.e. with an amorphous body in the interior which is yellowish or yellow in alkalic mounts and taking up cotton blue, in the latter case usually clavate or broadly ventricose with an apical mucro or neck and with thin wall; cheilocystidia always present; stipe central, squamose or naked, dry or viscid to glutinous; veil appendiculate or annulate, or almost absent in mature fruiting bodies; pigment often intraparietal or incrusting or dissolved or dissolving into a bright lemon yellow solution pervading the preparation,

\*The conservation of *Pholiota* is unnecessary if *Derminus* (Fr.) Staude is not recognized as a validly published generic name, or not typified the way Donk typified it. As both Rogers (1950) and I (1955, 1962) have pointed out, the status of the taxa raised to generic rank by Staude (1857) must be challenged; *Derminus* Fr. has no definable status, and Schröter's genus based on it was typified with a species belonging in *Crepidotus*.

\*\*The first author selecting rather than indicating (according to an outlawed code) a type species for *Flammula* is Konrad (1934): *F. alnicola*. Fayod's concept of *A. abruptus* is not the same as Karsten's, but refers to a *Pholiota* also (see also p. 619).

\*\*\*The type belongs in *Pholiota* sect. *Destruentes* as was suggested by Svrček, Kotlaba and Pouzar and by type studies (PR) by this author. The type specimen does have cheilocystidia. A second species published by Pilát is undoubtedly an *Agaricus* (*N. genezarthus* Pilát).

but if it also incrusts the epicutis elements, these are neither broad and organized in chains to form a trichodermium, nor in form of sphaerocysts, but more or less filamentous and bunched together in a peg-like manner to form the scales of the pielus; hyphae of the trama inamyloid, with clamp connections, often with gelatinized hymenopodium and epicutis; context sometimes bitter, but more often mild. On wood, grass roots, and generally dead fragments of Cormophyta, among moss (including in deep *Sphagnum*), on charcoal and ashes, on earth and humus, on dead and living trees, more rarely outside the woods and forests than inside; not ectotrophically mycorrhizal.

*Development of the carpophores:* Bivelangiocarpous and either stipitocarpous or pileostipitocarpous (Reijnders).

*Area:* Cosmopolitan.

*Limits:* *Pholiota* as emended by Singer & Smith and Singer (i.e. including the acystidiate and the exannulate, non-squamose species) differs from the other genera of Pholiotoideae according to the characters used in the key. The differences between *Stropharia* and *Pholiota* have been pointed out in that genus. The differences between *Pholiota* and *Naematoloma* and *Psilocybe* have been discussed under the latter two genera.

Smith & Hesler have emended the genus *Pholiota* more drastically than has been done by me. It is the merit of these authors to have added much detail to our knowledge of *Pholiota* and similar species in North America. The conclusions drawn from their observations are largely acceptable as far as they refer to *Pholiota* in the sense of Singer & Smith, Singer, Horak, Moser, Orton, Dennis, and other modern taxonomists. However, with regard to the limits of the genus the conclusions of Smith & Hesler have been unacceptable for me. In the first place, *Phaeolepiota* is not even related to *Pholiota*, a conviction which has been confirmed by the recent study of the fine structure of the spore wall and by a quantitative study of the whole of the characters. The genus *Kuehneromyces*, likewise, has been shown to have warty spores under the EM and can be distinguished from *Pholiota* without difficulties. For further comment see under *Kuehneromyces*, p. 385; The genus *Pachylepyrium* is distinguishable from *Pholiota* by several characters and so is *Phaeomarasmius*. The limits between both these genera and *Pholiota* are discussed under these two genera (*Phaeomarasmius* and *Pachylepyrium*).

*State of knowledge:* The data published recently by Smith & Hesler (1968) and, to a lesser degree myself on South American Pholiotas (various papers, especially 1969) have made it necessary to revise many species of this genus which has been done by me in order to provide a fully modernized infrageneric taxonomy of the Pholiotas. This was worked out by checking on the characters stressed by Smith & Hesler and found to be taxonomically valuable such as the behavior of the spore wall in Melzer's reagent, the structure of the spore apex (degree of continuity or discontinuity), the surface marking (adding now the EM findings by Pegler and Cléménçon), the exact colors of the spore prints, and the gelatinization of hymenopodial and epicuticular layers. While Smith & Hesler could not revise all these species studied by me, I could not revise all the species taken into account by Smith & Hesler, but the 75

species here recognized form an assemblage of well or sufficiently known forms which have made it possible to provide a skeletal but, I think, natural infrageneric classification. This classification will in the end absorb all those species which are still not fully known.

**Practical importance:** *P. destruens*, *P. aurivella* (especially *f. abietisnordmanniae*), and *P. squarrosoadisporsa* are very frequently active parasites and wood destroyers. They destroy trees in the forests as well as introduced park trees, and the mycelium continues its destruction after the tree is cut. Wooden bridges and similar wooden structures often deteriorate rapidly because of the action of certain basidiomycetes, among them Pholiotas. Few Pholiotas are edible, and even those are not widely known and little used. The only species with some market value is *P. nameko* (T. Ito) S. Ito & Imai, from Japan. It is now often commercially cultivated. On the other hand, Shaffer (1965) reported a thus far unconfirmed poisoning attributed to *P. squarrosa* and Hinttika (1978) found one sample of fresh mushroom toxic.

## SPECIES

**Subgenus I. Hemipholiota** Sing. (1951) ex Sing. (*Hebelomoides* Kühn. & Romagnesi 1953, *nom. nud.*). Pleurocystidia, none, or rare and scattered, and then not of the chrysocystidium-type and not incrusted or with stramineous walls; endocystidia and trama cells with chrysocystidiod contents or enclosures none; annulus mostly well developed; if the pileus is ± hygrophanous, the stipe is pallid; if the pileus is not scaly, the stipe is white or whitish (if yellow and hyphae with intercellular yellow pigment granulation - see subgenus *Pholiota*); spores not pseudoamyloid.

**Type species:** *P. destruens* (Brond.) Gillet.

Sect. 1. *DESTRUENTES* Konr. & Maubl. 1948. Pileus almost dry; spores with rounded apex (pileus with brown squarrose or squamose pileus, see subgenus II!).

**Type species:** *P. destruens* (Brond.) Gillet.

*P. destruens* (Brond.) Gillet. - Orton (1960) distinguishes from this species *P. heteroclita* (Fr. ex Fr.) Quél. and *P. comosa* (Fr.) Quél. *Nemecomyces mongolicus* Pilát belongs in this section and is obviously identical or close to one of the above named species, obviously also a much smaller species: *P. dissimilans* (Berk. & Br.) Sacc. (restudied by Singer and Orton, K.).

Sect. 2. *SORDIDAE* Sing. (1961). Pileus at first with a distinct, mostly persistent gelatinous epicutis, not thick-fleshy, neither squamulose nor squarrose, more or less hygrophanous, spores with a small germ pore, either truncate or non-truncate at the apex; stipe not yellow, but mostly white or whitish all over.

**Type species:** *Dryophila sordida* Kühn. & Romagnesi nom. nud. (= *P. oedipus* (Cooke) Orton).

*P. oedipus* (Cooke) Orton; *P. microcarpa* Sing.; *P. psathyelloides* Sing.; *P. agrocybiformis* Sing.; apparently also *P. brunnea* Smith & Hesler, *P. ochroflavida* Malençon in Malençon & Bertault; *P. discolor* (Peck) Sacc. and perhaps several other

North American species. - *Kuehneromyces macrosporus* Sing. is probably better placed in this section of *Pholiota*.\*

Sect. 3. *MYXANNULATAE* Hongo (1959). Annulus or veil glutinous or at least with a broad, strongly gelatinized hymenopodium in the trama of the lamellae; spores small (<7 µm with a very small (?) or no germ pore.

Type species: *P. nameko* (T. Ito) S. Ito & Imai.

*P. nameko* (T. Ito) S. Ito & Imai (Collybia, T. Ito; Kuehneromyces, S. Ito); perhaps also here *P. olivaceodisca* Smith & Hesler (although stipe and veil not described as viscid and with peculiar spore color: "Isabella color" Ridgway).

Sect. 4. *ALBOCRENULATAE* Sing. (1961). Pileus with broad, appressed squamose patches, viscid; spores with subacute apex, rather large (>10 µm).

Type species: *P. albocrenulata* (Peck) Sacc.

*P. albocrenulata* (Peck) Sacc. (Stropharia, Kreisel & Lazebníček; *P. fusca* Quél.).

Subgenus II. **Pholiota** (*Eupholiota* Lange 1938). Pleurocystidia present in form of thin-walled cystidia, often excluding a yellow or brownish mass and incrusted by it, or in form of metuloids or chrysocystidia, rarely almost or quite absent and then stipe yellow and a yellow intercellular granulosity present; pileus squamose or squarrose, more rarely only slightly squamulose-fibrillose (but if only small fugacious fibrillose scales are present and the epicutis is gelatinized, see subgenus III), sometimes with conspicuous but detersile pigmented floccos; stipe annulate, but the annular veil is often either fugacious or indistinctly delimiting the squamose lower part of the stipe; usually growing on wood, even on living trees or their base, few species on the ground. - Spores not pseudoamyloid.

Type species: *P. squarrosa* (Pers. ex Fr.) Kummer.

Sect. 5. *FLAVIDULA* Smith & Hesler (1968). Pleurocystidia generally indistinct or absent; epicutis as well as hymenopodium non-gelatinized; spores only up to 9.5 µm large; surface of the pileus becoming cinnamon or rusty ("Mohawk" M & P) with KOH; pigments predominantly bright lemon yellow in pileus and stipe or hyphae excluding yellow pigment in KOH mounts, intercellular yellow pigment typically abundant; odor none; taste mild to bitter.

Type species: *P. curvipes* (Fr.) Quél.

*P. tuberculosa* (Schaeffer ex Fr.) Kummer; *P. curvipes* (Fr.) Quél.; probably also *P. multifolia* (Peck) Smith & Hesler and *P. subsulphurea* Smith & Hesler; possibly also *P. murrillii* Smith & Hesler (certainly not a *Phaeomarasmius*).

Sect. 6. *PHOLIOTA* (*Squarrosae* Konr. & Maubl. 1937). Pleurocystidia distinct in form of chrysocystidia; pileus not glutinous or viscid and no glutinous layer in the cuticular region; hymenopodium not gelatinized; odor often strong; taste not bitter.

Type species: *P. squarrosa* (Fr.) Kummer.

\*Horak (1979) who describes and illustrates *Pholiota megalospora* Sing. indicated *K. macrosporus* as a synonym. But this latter species has no pleurocystidia, has a distinctly hygrophanous pileus and is never lignicolous.

*P. squarrosa* (Fr.) Kummer.

Sect. 7. *ADIPOSAE* Konr. & Maubl. (1948). Both cuticle and hymenopodium gelatinized in mature carpophores; otherwise much like the preceding section; odor agreeable or none; taste not bitter but sometimes slightly acrid.

Type species: *P. adiposa* (Fr.) Kummer.

Stirps *Squarrosoides*. (Gelatinous layer becoming evident underneath the scales at maturity, the scales appressed or more often squarrose, usually persistent.)

*P. ochropallida* (Romagnesi) Moser in Gams\*; *P. squarrosooides* (Peck) Sacc.; *P. terrestris* Overholts; *P. angustifolia* Smith & Hesler (*Hebeloma appendiculatum* Murr.); perhaps also *Hypoloma polylepidis* Dennis.

Stirps *Subflammans* (= sect. *Subflammantes* Sing. 1961). Scales at first conspicuous and floccose-squarrose, erect, separable, eventually disappearing because of the strongly gelatinous underlying epicuticular layer and early obliterated by rain and in age, stramineous to yellow-brown or yellow, not tending to rusty-orange-red nor to warm sepia or violet brown; spores generally small (<8.8  $\mu\text{m}$ ).

Note: These species, after heavy rain, may be looked for under subgenus *Flammula*.

*P. subflammans* (Speg.) Sacc.; *P. digilioi* Sing.; *P. flammans* (Fr.) Kummer.

Stirps *Adiposa*. (Gelatinous layer - epicutis - not obscured in young specimens by the non-gelatinous tissue of the scales (general veil), the latter appressed or squarrose, if squarrose - quite persistent; spores small or large.

*P. aurivella* (Fr.) Kummer; *P. aurivelloides* Overholts; *P. squarrosoadiposa* Lange; *P. adiposa* (Fr.) Kummer; apparently also *P. lucifera* (Lasch) Quél. (sensu Fayod, Sing., Kühner & Romagnesi, Smith & Hesler) - although the chrysocystidia may be rare or perhaps absent but then replaced by endocystidia with chrysocystidioid contents); also *P. maackiae* Sing. and obviously *P. limonella* (Peck) Sacc. and *P. tennesseensis* Smith & Hesler.

Subgenus III. *Flammula* (Fr. ex Fr.) Sing. (Subgenus *Flammuloides* Smith & Hesler). Pleurocystidia always present unless the spores are (weakly) pseudoamyloid, either as chrysocystidia or as prominent leptocystidia or metuloids or both; pileus not scaly if only chrysocystidia are present, or if no pleurocystidia are present at all but sometimes there are white or pallid velar floccos on the surface of the pileus which tend to disappear later but in this case conspicuous non-chrysocystidioid pleurocystidia present; veil usually not annular (excepting some species in sect. *Albivelatae* and in stirps *Lubrica*). Habit often similar to that of *Stropharia* or *Naematoloma*. On wood, but also sometimes on earth, charcoal, grass roots, in deep moss (incl. *Sphagnum*) etc.

Type species: *Pholiota alnicola* (Fr.) Sing.

\*It appears that Smith & Hesler (1968) took the heliotrop odor indicated by Romagnesi for heliotrop stains; thus, *P. romagnesiana* Smith & Hesler differs only very slightly from the European species and is probably identical.

Sect. 8. UDAE (Fr.) Sing. (1951). Pleurocystidia (all kinds) absent; spores more or less strongly pseudoamyloid (assuming a somewhat reddish tone when mounted in Melzer's reagent and compared with spores in NH<sub>4</sub>OH); pileus naked; stipe exannulate.

Type species: *Pholiota flavidula* (Schaeff. ex Fr.) Sing.

*P. flavidula* (Schaeff. ex Fr.) Sing.; *P. aromatica* Orton (*P. pseudohypholoma* Velen.?); *P. malicola* (Kauffm.) A.H. Smith (*Flammula sulphurea* Peck); *P. alnicola* (Fr.) Sing. (*P. apicrea* (Fr.) Moser in Gams sensu Lange vix sensu Moser); *P. amara* (Bull. ex St-Amans) Sing (*Flammula*, *Turconi*; *P. alnicola* (Fr.) Sing. sensu Konr. & Maubl.; Smith & Hesler).

Sect. 9. *ALBIVELATAE* Smith & Hesler (1968). Pleurocystidia always present in the form of chrysocystidia (more or less typical); epicutis gelatinized or not, but even if the epicutis is gelatinized, the hymenopodium is not or scarcely gelatinized; stipe mostly with a more or less persistent white or whitish membranous annulus; base of stipe usually with conspicuous white rhizomorphs.

Type species: *P. albivelata* Murr.

*P. albivelata* Murr.; *P. apiahyna* Speg. (*Pholiota carneola* Rick); apparently also here *P. durooides* Peck; *P. pseudofascicularis* Speg. (*Inocybe caespitosella* Speg.).

Note: This section as well as the subgenus *Phaenonematoloma* are the groups within *Pholiota* where the spore print colors vary most, thus, where "transitions" to *Stropharia* respectively *Naematoloma* occur.

Sect. 10. *SUBSICCAE* (Lange) Sing. (1973). (*Flammula* sect. *Subsiccae* Lange 1939). Differs from the preceding section in the absence of a white or whitish membranous annulus; epicutis - an ixocutis.

Type species: *P. astragalina* (Fr.) Sing.

Subsection *Astragalinae* Sing. (1973). Epicutis gelatinized (weakly to strongly) but pileus not glutinous; hymenopodium not gelatinized; chrysocystidia large. On wood and on such hosts as *Phragmites*, *Imperata*, *Scirpus*.

Type species: *P. astragalina* (Fr.) Sing.

*P. astragalina* (Fr.) Sing.; *P. lутaria* (Maire) Sing. (*Tubaria*, *Maire*; *Flammula graminis* (Quél.) Sing.; *Dryophila*, Kühner & Romagnesi; *D. muricella* (Fr.) Quél. sensu Quél. 1888 non Fr.); *P. aurantioalbida* Sing.; *P. subochracea* (A.H. Smith) Smith & Hesler; *P. calendulina* Sing. (unless rather to the following subsection); perhaps *P. helicocae* (Berk. & Br.) Sing. (*Naucoria*, *Sacc.*).

Subsection *Gummosinae* Sing. (1973). Pileus strongly viscid to glutinous; hymenopodium gelatinized; chrysocystidia basidiomorphous or normal (clavate-ventricose and mucronate) shaped, not particularly large, with or without a solid amorphous body; on soil as well as on dead wood, often cespitose, also among fallen leaves.

Type species: *P. gummosa* (Lasch) Sing.

*P. gummosa* (Lasch) Sing. (sensu Romagnesi); *P. ascophora* (Peck) Sing.; obviously

also some other North American species such as *P. burkei* Smith & Hesler, *P. lutescens* Smith & Hesler.

Sect. 11. DELUBRICATAE Sing. (1973). Cystidial characters of sect. *Lubricae*; hyphal characters of sect. *Albivelatae*; spores rather large (<9.5  $\mu\text{m}$ ).

Type and only known species: *P. marthae* Sing.

Sect. 12. LUBRICAE (Fr.) Sing. (1951). Subgen. and sect. *Flammuloides* Smith & Hesler 1968; Subgen. *Flammula* section *Sericellae* (Fr.) Sing. 1961; trib. *Flammula* sect. *Sericellae*.) Instead of or together with chrysocystidia there are also conspicuous pleurocystidia of another type (lepto- or metuloid cystidia); otherwise like section *Subsiccae*; epicutis - an ixocutis.

Type species: *P. lubrica* (Fr.) Sing.

Subsection *Privignae* (Sing.) Sing. (1973). (Subgen. *Flammuloides* sect. *Flammuloides* Smith & Hesler.) Pleurocystidia conspicuous, often metuloid (with more or less thickened walls); sometimes these with chrysocystidioid contents, or chrysocystidia also present; hymenopodium ± gelatinized. On earth, wood, sphagnum, and charcoal.

Type species: *P. privigna* (Speg.) Sing.

*P. montana* Sing. in Sing. & Moser; *P. privigna* (Speg.) Sing.; *P. chrysocystidiata* Sing. ex Sing. nom. nov. (*P. spumosa* var. *chrysocystidiophora* Sing. *Nov. Hedw.*, *Beih.* 29: 274. 1964.); *P. condensa* (Peck) Smith & Hesler (*P. spumosa* var. *crassitunicata* Sing.); *P. baeosperma* Sing.; *P. iterata* Smith & Hesler. Perhaps also here: *P. alnea* Sing.

Subsection *Spumosinae* Sing. (1948). (Sect. *Spumosae* Smith & Hesler). Pleurocystidia thin-walled; chrysocystidia none or extremely scarce.

Type species: *P. spumosa* (Fr.) Sing.

Stirps *Carbonicola*. (Growing preferably or exclusively on burnt ground, charcoal and ashes. Spores 5-9  $\times$  3.5-5  $\mu\text{m}$ ).

*P. carbonaria* (Fr.) Sing. (*Flammula*, Kummer; *Pholiota highlandensis* (Peck) Smith & Hesler sensu Peck, Smith & Hesler, non Kauffm.); *P. carbonicola* A.H. Smith ex Sing.\*; obviously also some other North American species.

Stirps *Sphagnicola*. (Sphagnicolous species).

*P. kubickae* Sing. & Clémenton; *P. chromacystis* Smith & Hesler; obviously also *P. sphagnicola* (Peck) Smith & Hesler and perhaps some other North American species.

Stirps *Spumosa*. (Not carbonicolous and not sphagnicolous. Spores generally more than 7  $\mu\text{m}$  long).

\*A.H. Smith in his original protolog referred to this species as to *P. carbonaria* and as *P. carbonicola*. According to the Code of Nomenclature this invalidates the effectiveness of the publication; the species was first validated by Singer (1962) as *P. carbonicola* (= *P. carbonaria/carbonicola* A.H. Smith, *Mycologia* 36: 253. 1944).

*P. spumosa* (Fr.) Sing. (sensu Smith & Hesler); *P. scamba* (Fr.) Moser in Gams; *P. megalospora* Sing.; also some North American species (not known to this author).

Stirps *Lubrica*. (Spores generally small: 5-8-(9)  $\mu\text{m}$ ; neither carbonicolous nor sphagnicolous; veil sometimes strongly developed and viscid; spore print sometimes rather dark.)

*P. lubrica* (Fr.) Sing.; *P. lenta* (Fr.) Sing.; *P. glutinipes* Sing. in Dennis; *P. freindlingiae* (Sing.) Sing.; *P. polychroa* (Berk.) Smith & Brodie; *P. appendiculata* Peck (unless too close to the preceding species).

Subgenus IV. *PHAEONEMATOLOMA* (Sing.) Sing. (1951). Differs from the preceding subgenus in the covering of the stipe or the veil on the stipe which is glutinous, consisting of scattered filamentous hyphae imbedded in a copious glutinous mass; if pleurocystidia other than chrysocystidia are present, the spores are large (9-14  $\mu\text{m}$  - (small-spored cystidiate species with glutinous veil cf. stirps *Lubrica*); spore print often rather dark or violet brown (but not always).

*Type species: P. myosotis* (Fr.) Sing.

Sect. 13. *GLUTINIGERA* Sing. (1960). Chrysocystidia present but conspicuous non-chrysocystidioid cystidia absent.

*Type species: P. myosotis* (Fr.) Sing.

Stirps *Myosotis*. (Spores large,  $>14 \mu\text{m}$ ; stipe only with a viscid veil or veil zones; growing in Sphagneta and in boggy soil; stipe often relatively long.)

*P. myosotis* (Fr.) Sing. (Naucoria, Kummer; Naematoloma, A.H. Smith); *P. lapponica* (Fr.) Sing.; probably also *Flammula lenticeps* Sing.

Stirps *Silvatica*. (Spores  $>8 \mu\text{m}$ ,  $<13.5 \mu\text{m}$ ; growing on humus in the forests or among *Polytrichum*.)

*P. aberrans* Smith & Hesler (Naematoloma anomalam (A.H. Smith) A.H. Smith; *Pholiota*, Sing. 1961 non Peck 1895); *P. glutinigera* Sing.; *P. myxacioides* Sing.; apparently also *P. silvatica* (A.H. Smith) Smith & Hesler and *Naematoloma viscidipes* (A.H. Smith) A.H. Smith.

Stirps *Fowardii*. (Spores smaller than 8  $\mu\text{m}$ ; growing among fallen leaves in forests.)

*P. fowardii* (Speg.) Horak.

Sect. 14. *NOVEMBERES* Sing. (1973). Chrysocystidia present though sometimes scarce; besides there are also conspicuous, often metuloid pleurocystidia.

*Type species: P. nobembris* Sing.

*P. novembbris* Sing.; *P. majalis* Sing.

*Note:* I have originally inserted the Myosotis-group in *Flammula* respectively *Pholiota*; later, influenced by A.H. Smith's and my own observations on the exact color of the spore print, transferred it to the Stropharioideae but retransferred it recently to *Pholiota* since, as a whole, it comes closer to *Pholiota* than to *Naematoloma* and

a gradual transition in spore color from one species to the other can be noticed. This coincides with Smith & Hesler's present position.

Subgenus V. **Plocoloma** Sing. (1965). Minute to small carpophores with fibrillose-squarrulose, tomentose pileus and stipe; chrysocystidia and metuloids none, but other types of pleurocystidia well differentiated; lamellulae typically none or few; annulus none. On Pteridophyta, perhaps also on dicotyledonous bark.

*Types species: P. blechni* Sing. in Sing. & Moser.

*P. blechni* Sing. in Sing. & Moser. Probably also *P. pseudolimulata* Smith & Hesler; *P. cyathicola* (Murr.) Smith & Hesler; *P. corticola* (Murr.) Smith & Hesler; *P. naucoroides* Sing. (the last four species closely related with each other, but aside from the last one not known to me),

**Note:** A number of obviously good species of *Pholiota* could not yet be placed in the scheme of infrageneric taxa distinguished above. These are: *P. bicolor* (Speg.) Sing.; *P. rufipunctata* (Berk. & Br.) Sing. (*Flammula*, Sacc. 5: 819. 1887); *P. spinulifera* (Murr.) Sing.

### 163. KUEHNEROMYCES Sing. & Smith

*Mycologia* 38: 504. 1946.

*Type species: Kuehneromyces mutabilis* (Schaeff. & Fr.) Sing. & Smith.

**Characters:** Pileus glabrous, naked, opimus to subviscid but not glutinous, hygrophanous all over with mostly transparently striate margin, mostly ochraceous to cinnamon or brown, perhaps with olive or red or yellow shades; epicutis consisting of sub-parallel, repent, thin-filamentous, hyaline hyphae which are more often gelatinized than not, with clamp connections; hypodermium consisting of more irregular, rather broad, eventually often thick-walled hyphae with faint to strong pigment-incrustations; dermatocystidia none on the pileus, but mostly present on the stipe; lamellae variously attached, never free; spore print color cinnamon brown or rusty brown (Seguy between 176 and 191; between "Verona brown" and "cinnamon brown" or near "snuff brown" or "Brussels brown" of Ridgway; between "Cochin" and "Sudan br." or as deep as between "Cochin" and "Mandalay" M & P; Methuen Handbood of Colour 6-E-8); spores in KOH melleous to brownish ochraceous or ochraceous brown, with complex\* wall, with a usually broad and truncate germ pore, ovoid or ellipsoid, rarely slightly oblong, not or very slightly lentiform, not or very slightly bean shaped, not over 11  $\mu\text{m}$  long, under the light microscope quite smooth but in EM - verrucose from tuberculate outgrowths; basidia normal; cheilocystidia present; pleurocystidia mostly absent, rarely present and then neither chrysocystidoid nor metuloid but of the type of the cheilocystidia which may be of two types or uniformly shaped; hymenophoral trama regular; stipe

\*In the main layer of the coriotunica, corresponding to part of the episporium in light microscopy, there is a cup ("Kelch") imbedded which starts from the apiculus (hilar appendage) as an EM-light structure and reaches variable distances upward within the coriotunica (Cléménçon 1974).

central, usually pigmented but not bright lemon yellow, sometimes fasciculate, stuffed, eventually hollow, not over 12 mm broad, mostly much narrower, squamulose or squarrose, or naked, but often annulate from a partial veil, but also exannulate and even without any traces of a veil in mature specimens (veil extremely fugacious); context of the pileus fleshy but often rather thin, not gelatinized; hymenopodium likewise not gelatinized. On wood, sawdust, volcanic ashes over soil, rarely on humus, often vernal. Pl. 68B, 1-3, 6-7.

*Development of the carpophores:* Bivelangiocarpous.

*Area:* In the temperate zones of the Northern and Southern Hemisphere, also in the tropics and subtropics (there usually in the montane zone).

*Limits:* *Kuehneromyces* differs from *Pholiota* subgenus *Hemipholiota* in habit, strongly hygrophanous and transparently striate, naked pileus, rarely pallid stipe; the spores are apically truncate from a germ pore. *Pholiota* section *Myxannulatae* has glutinous pileus and gelatinized hymenopodium. *Pholiota* sect. *Flavidula* differs in the intercellular bright yellow pigment of the stipe (among other characters) and does not appear to be related to *Kuehneromyces*. *Pholiota* sect. *Flammula* differs in the more or less pseudoamyloid spores and the weakly or non-hygrophanous pileus; *Pholiota* section *Lubricae* subsection *Spumosinae* is, because of the presence of cystidia, comparable to *K. cistidiosus* which differs amply from the respective *Pholiotas* by all other but the cystidial characters. Furthermore, if the data for *K. mutabilis*, the type species, could be generalized, the spores are warty in electron microscope sections (Cléménçon 1972) and in scanning microscope photos (Pegler & Young) which is not the case in any of the *Pholiotas* studied until now.

According to a survey by Cléménçon (*Zeitschr. f. Mykol.* 40: 105-126. 1974) only two species of *Kuehneromyces* (viz. *K. mutabilis* and *K. populicola* (Smith & Hesler show the characteristic ornaments on the spores in EM sections, and the most constant differences between *Pholiota* and *Kuehneromyces* is the "Kuehneromyces-Kelch" (l.c. fig. 1, p. 114) which, aside from *Kuehneromyces* can only be found in *P. tennesseensis* and *P. carbonaria* which differ, on the other hand, from all *Kuehneromyces* species in nearly all diagnostic characters indicated for the latter genus and are not closely related to any species of *Kuehneromyces* because of the germ pore structure and presence of conspicuous pleurocystidia of the *Pholiota*-type. It is therefore possible to confirm the separation of *Kuehneromyces* from *Pholiota* by EM-derived characters in two possible ways, either by the presence of the "Kuehneromyces-Kelch" which permits a wider concept of the genus, or by the ornamentation which would indicate a smaller genus. If the latter attitude should be preferred, the EM-smooth-spored species would mostly pass to the nearest group in *Pholiota* viz. sect. *Sordidae*. I believe that at present it is better to accept *Kuehneromyces* in the wider sense as does Cléménçon (l.c. p. 113. "The spore wall structures suggest that *Kuehneromyces* and *Pholiota* are different but closely related genera") inasmuch as the ultrastructure of the spore walls of species of sect. *Sordidae* has not been studied sufficiently.

As for *Kuehneromyces* versus *Psilocybe*, see under the latter genus (p. 567).

The arguments given by Orton (1960) in favor of combining *Kuehneromyces* with *Galerina*, or those given by Smith & Hesler (1968) in favor of combining *Kuehneromyces* with *Pholiota* are not acceptable. With regard to Orton's disposal of *Kuehneromyces*, it must be emphasized that even those species of *Galerina* which have a small germ pore have completely different wall structure. The approximation of the spores of both genera has also been rejected by Pegler & Young (*Trans. Brit. Myc. Soc.* 52: 495. 1969) and Clémençon (l.c.) on the basis of spore ultrastructure. The only species where an intermediate position might be assumed is *Galerina nybergii* A.H. Smith in Smith & Sing. which has been rediscovered by me in the Alps, and which might be compared with *Kuehneromyces macrosporus* Sing. which, however, is rather a *Pholiota* see p. 579). A closer comparison shows that the spores are relatively much broader in *K. macrosporus*, as they are generally in *Kuehneromyces*, the germ pore consistently broader, the spore print color cinnamon brown as in *K. mutabilis*, the epicutis gelatinized as in most species of *Kuehneromyces*; the lamellae have a grayish to argillaceous color as rarely found in *Galerina* when young; on the other hand *G. nybergii* has relatively narrow ( $Q > 2$ ) spores as often in *Galerina* and the germ pore is narrow, only in few spores relatively broad and somewhat truncate; the spore print and lamellae color like that of the majority of Galerinas; and there is no gelatinized epicutis present - a condition rarely encountered in typical *Kuehneromyces*. All other smooth-spored Galerinas can be easily distinguished from *Kuehneromyces* by either marbled or much larger or pseudoamyloid spores whereas in *Kuehneromyces* they are only up to 11  $\mu\text{m}$  long, never marbled and never pseudoamyloid. Smith & Hesler are in agreement with this view insofar as they consider *Galerina* to be generically different from *Kuehneromyces* (their section *Kuehneromyces* of *Pholiota*).

However, by incorporating *Kuehneromyces* in their genus *Pholiota*, these authors differ from the generic taxonomy of Orton, Moser, Dennis, Smith & Singer, and my own, only to return to an earlier, basically Friesian, classification. They support their view by filling the gaps between the two genera with frequently insufficiently described or insufficiently known species - a procedure obviously inevitable in a monograph aimed at completeness, but not convincing for purposes of delimitation of genera. They say (p. 87) that it is because of species as *P. davidsonii* that *Kuehneromyces* had to be abandoned; yet, *P. davidsonii* is described without indication of the hygrophanity or striation of the pileus, the color of the spore print, and the species is described from "dried, immature" material of a single collection. Furthermore, the section *Mutabiles* contains species obviously foreign to *Kuehneromyces* viz. *P. tennesseensis* which, according to its description would key out in Smith & Hesler's main key (p. 38) with subgenus *Pholiota* (not subgenus *Hemipholiota*) where, indeed it apparently belongs (close to *P. lucifera*). Clémençon (l.c.) includes this species in the list of species having spores with a *Kuehneromyces*-Kelch which would suggest that, like *P. carbonaria*, some otherwise non-related species of *Pholiota* share this structure with *Kuehneromyces*. In their discussion of the "evolutionary tendencies", the authors simplify the problem to such a degree that it might appear as if *Kuehneromyces* were what they call "*Pholiota*-species with truncate spores". No doubt, there are several good *Pholiota*-species with truncate spores since this character is by no means the only one on which *Kuehneromyces* was based.

in the first place; on the other hand some of the species entering sect. *Mutabiles* in Smith & Hesler, lack truncate spores ("obscurely" or "slightly" truncate).

In reality the question boils down to a simple decision: Is *Pholiota* sect. *Sordidae* separated from *Kuehneromyces* by a hiatus of reasonable size? The differences mentioned by me above - hygrophanity, striation, viscosity, color of the stipe and truncation of the spores - are all helpful but they are neither characters of the highest general value nor are they absolute and qualitative. The transparent striation of the margin is nil in *P. agrocybiformis* and *P. microcarpa*, short and inconstant in *P. oedipus* and *P. psathyelloides*. All species are somewhat viscid to glutinous; all are either non-hygrophanous or very weakly and partially (in the marginal region) hygrophanous. All species have a remarkably narrow only inconsistently truncate (in a minority of spores) germ pore. The stipe is white or pallid in all species, but browning where handled in *P. oedipus* and *P. microcarpa*. *Kuehneromyces* is non-viscid to subviscid, always strongly and thoroughly hygrophanous, mostly (except in *K. macrosporus*) at least over one quarter of the radius transparently striate when mature and wet. The spores are in all species known to me provided with a truncate broad germ pore, but Smith & Hesler say that the spores are "obscurely truncate" in *K. vernalis* which is in contrast to my notes on this species. The stipe of all species of *Kuehneromyces* known to me is pigmented even though Peck states about his *Pholiota marginella* that the stipe is pallid or whitish (*K. lignicola* (Peck) Redhead and *Gymnopilus hillii* Murr. sec. Redhead). If we look for further differences, we note that the spores of *Kuehneromyces* are never phaseoliform whereas in *Pholiota* sect. *Sordidae* at least a minority of such spores is certainly found in *P. oedipus* and *P. microspora*, and perhaps in the other species. Taking all this in conjunction with a generalisation of the findings on the EM characteristics of the spores, I believe that the hiatus between *Kuehneromyces* and *Pholiota* on this level is well enough in evidence.

*State of knowledge:* 8 species are now recognized in *Kuehneromyces*.

*Practical importance:* Probably all species are edible but the one widely used for food is *K. mutabilis*. This species frequently occurs on structural timber, such as wooden bridges, but it does not destroy healthy wood; at least at the time it forms carpophores, the wood is usually already strongly decomposed. However, it was found to cause a strong red-brown pulp rot on *Picea* in Norway (Friesia 1: 91. 1933).

## SPECIES

### 1. Typical species with EM-verrucose spores:

*K. mutabilis* (Schaeff. ex Fr.) Sing. & Sm.; *K. populicola* (Smith & Hesler) Sing.\*

### 2. Species with SM-smooth spores and species for which EM data are missing.

*K. vernalis* (Peck) Sing. & Sm.; *K. marginellus* (Peck) Redhead (*K. rostratus* Sing. & Smith); *K. castaneiceps* Sing.; *K. cystidiosus* Sing.; *K. nudus* Sing.; *K. vinicolor* (Pat.) Pegler; apparently also *K. myriadophylla* (Orton) Pegler & Young (unless too

\*c.n. (*Pholiota populicola* Smith & Hesler, *North Amer. Spec. Pholiota*, p. 120. 1968).

close to *K. vernalis*) and *Pholiota galerinoides* Sm. & Hesler (but this and especially *K. depauperatus* Sing. & Smith might belong to *Psilocybe* - spore prints not obtained).

## 164. PACHYLEPYRIUM Sing.

*Sydowia* 11: 321. 1957.

*Type species: Pachylepyrium fulvidula* (Sing. in Sing. & Digilio) Sing.

**Characters:** Habit naucoroid and in appearance much like *Gymnopilus* or *Kuehneromyces*. Pileus hygrophanous or dry and then fading in age; stipe veiled (but annulus not well differentiated), central, long, not curved and sometimes partly buried in the earth like *Battarrea*, the subterranean part taking the function of a pseudorrhiza. Spores very intensely pigmented (much deeper under the microscope than in *Kühneromyces*), not ornamented, very thick-walled, at times appearing angular-rhomboid but also often normally ellipsoid, with germ pore which is either broad and truncate or narrow and not truncate, with the suprahilar region not depressed, medium to large ( $7.5-14 \mu\text{m}$ ), wall  $0.7-1.7 \mu\text{m}$  thick when mature, if not brightly colored in KOH mounts, the spore print is very bright rufous-red-brown or intensely rust color; basidia normal, hymenophore regular, not with gelatinized hymenopodium; hyphae with clamp connections; epicutis of the pileus a cutis, but some hyphae ascendant (sometimes in fascicles which form scales), not gelatinized; pleurocystidia, chrysocystidia, metuloids - none; veil sometimes annuliform, but annulus neither persistent nor consistent, often absent and veil frequently more distinct on the pileus, especially the margin. On deeply immersed stems and roots in loose earth, on dead tree trunks, and on charcoal, often in xerophytic, or on the contrary excessively hygrophilous vegetation or in *Funaria*-associations.

**Development of the carpophores:** Apparently "hemiangiocarpous" but not studied in detail.

**Area:** Widely distributed in burned areas in Europe and North America but also in dry regions as well as very wet zones (cloud forest, subpáramo) in the tropics and Southern South America.

**Limits:** Smith & Hesler (1968) place this genus - without knowing the type species - in their subgenus *Hygrotrama* of *Pholiota* (an assemblage of species belonging in *Pholiota*, *Phaeomarasmius*, *Phaeolepiota* and *Pachylepyrium* of my classification). There is an obvious contradiction in the argument rejecting the spore wall thickness when these authors (incorrectly) claim (p. 44) that "in all the stirpes so far discussed for this subgenus the spores approach those of *P. subangularis*" [= *Pachylepyrium carbonicola*] while on this (p. 44) and the following page (p. 45) they state that in this very species the spores have "thicker spore walls than occurs in other stirps..." and have "a thick wall for the genus" [*Pholiota*]. The fact that in *Rhizopogon* the spore walls vary from 0.5 to over  $1.5 \mu\text{m}$  thick is hardly relevant for the case at hand. It is furthermore impossible, here as in the case of *Kuehneromyces*, to consider only one character of a genus. The relatively thicker spore walls and the spore colors are correlated in *Pachylepyrium* with the absence of cystidia, non-gelatinized

epicutis, medium to large spore size, presence of a germ pore, and a rather specialized ecology. None of the species of *Pachylepyrium* is close or similar to any of the acystidiate sections of *Pholiota* or, for that matter *Phaeomarasmius* or *Pleuroflammula*. The latter genus is the one most closely related to *Pachylepyrium* but differs sharply in its pleurotoid habit.

The relatively deep and bright pigmentation of the spores may possibly lead to confusion with Cortinarieae (Cortinariaceae), especially species of *Phaeocollybia* with "subsmooth" spores. But aside from the fact that in the latter genus the spores are ornamented even in subsmooth spores, the habit of the carpophores (papillate to umbonate) and the presence of a georrhiza (stipe decidedly attenuate-radican at base) should always be sufficient to make the correct generic identification.

*State of knowledge:* Five species are now recognized in this genus.

*Practical importance:* Unknown.

## SPECIES

*P. fulvidula* (Sing.) Sing.; *P. nubicola* Sing. in Dennis; *P. funariophilum* (Moser) Sing. in Moser & Sing.; *P. carbonicola* (A.H. Smith) Sing. (Kuehneromyces, A.H. Smith; *Pholiota subangularis* Smith & Hesler); *P. squarrulosum* Sing.

### 165. PLEUROFLAMMULA Sing. apud Sing. & Sm.

*Mycologia* 38: 521. 1946.

*Type species:* *P. dussii* (Pat.) Sing.

*Characters:* Pileus yellowish to rich chestnut brown, often both colors present, fibrillose-subtomentose to glabrous, non-viscid, non-hygrophanous to subhygrophanous, small; epicutis consisting of repent hyphae with or without pigment incrustations or at least with membrana-pigment, some of the terminal members of the epicuticular hyphae at times assuming the shape of dermatocystidia but very scattered; spore print "Brussels brown" (Ridgway) to brighter ferruginous; spores a rich deep rusty cinnamon or rusty-ochraceous when seen in KOH, smooth, with distinctly double (episporium and endosporium) wall, very broadly rounded below with the hilar end little marked, the apex with a very indistinct to distinct germ pore but rarely truncate and even then only indistinctly so, small to moderately large (Pl. 68, B, 5); hyphae of the young hymenophoral trama regular with very thin-walled hyphae; cheilocystidia (Pl. 63, B, 4) always present and very conspicuous, hyaline, very rarely a few cheilocystidia assuming the character of chrysocystidia; pleurocystidia none; stipe - if present - very short (shorter than the diameter of the pileus), curved in all specimens and often touching the margin of the pileus, eccentric to almost lateral; veil present (or sometimes absent?); context consisting of a fleshy trama; hyphae with clamp connections; in some species, there is a bright and rich colored (yellow) pigment, probably of intercellular origin, that is easily dissolved in

ammonia and finally dyes all the cells of the preparation containing it. On various frondose trees and shrubs, mostly on dry limbs and on fallen branches, logs, etc.

*Development of the carpophores:* Probably "hemiangiocarpous", not known in detail.

*Area:* North, Central, and South America, in the temperate, subtropical, and tropical zone of both hemispheres, the northern as well as the southern; also in the eastern hemisphere (Atlantic floral district, India; Far East).

*Limits:* This genus differs amply from all genera of this group. It also differs from the analogous genus *Melanotus* which has purplish fuscous or deep lilac spore print and lacks the yellow soluble pigment of many *Pleuroflammulae*. The cheilocystidia have another shape and the spores are more intensely colored and never lentiform nor do they always have a truncate germ pore as they have (at least the majority of the spores) in *Melanotus*. Both *Melanotus* and *Pleuroflammula* have often been confused with *Crepidotus* but all smooth-spored species of *Crepidotus* are widely different from the pleurotoid strophariaceous genera and no affinity can be discovered between any to the *Crepidoti* and any of the *Pleuroflammulae* even those in which thus far no veiled stage has been recovered, or where the stipe appears to be rudimentary.

*State of knowledge:* Ten species are now recognized in *Pleuroflammula*.

*Practical importance:* Unknown.

## SPECIES

*P. majuscula* Sing.; *P. croceosanguinea* (Mont.) Sing.; *P. fluminensis* Sing.; *P. dussii* (Pat.) Sing.; *P. filifera* Sing.; *P. flavomarginata* (Berk. & Br.) Sing.; *P. flammea* (Murr.) Sing.; *P. squarrulosa* Sing.; *P. chocoruensis* Sing.; *P. ragazziana* (Bres.) Horak (*P. hiberniana* (Pearson & Dennis in Pearson) Sing.; *P. austroafri-canus* (Pilát) Reid); obviously also *P. overeemii* Horak; *P. praestans* Horak, and *P. simulans* Horak.

## 166. PHAEOMARASMIUS Scherffel

*Hedwigia* 36: 289. 1897; em.

*Type species:* *P. excentricus* Scherffel.

*Syn.:* *Marasmiopsis* Henn. in Engl. & Prantl, *Nat. Pfl.-fam.* 1 (1\*\*); 230. 1898.

*Flammulaster* Earle, *Bull. N. Y. Bot. Gard.* 5: 435. 1909.

*Epicorticium* Vel., *Mykologia* 3: 72. 1926.

*Flocculina* Orton, *Brit. Mycol. Soc. Trans.* 43: 168. 1960.

*Characters:* Habit collybioid-marasmoid and often somewhat pleurotoid, or else collybioid; pileus non-viscid and more frequently non-hygrophanous than hygrophanous, beset with small punctations, floccons, or squamules of a covering layer

which is deep and richly colored (fulvous-rufous, etc.), or else evenly subvelutinous or furfuraceous and glabrescent; epicutis an (often disrupted) trichodermium, the terminal members of the hyphal chains mostly dermatocystidioid, or many of the members very strongly shortened, with an epithelium-like structure resulting, mostly incrusted by pigment (Pl. 74 Me) pileus at first convex, often semiglobose, margin often sulcate; lamellae adnate to subfree, distant or subdistant, more rarely subclose, always with pallid edge when fresh and seen under a lens; basidia normal but often bisporous, cystidia on the sides of the lamellae none, or rarely scattered cheilocystidia reaching part way up from the edges which are heteromorphous; cheilocystidia always present, conspicuous; spores in print from as light colored as "Nankeen" to between "spruce yellow" and "Inca gold", 11-F-4 (Maerz & Paul), or reaching Séguy 336 "buckthorn brown" (Ridgway), between "burnt umber" and "Alamo", or from "Arab" to "Cognac" or "raw sienna" (Maerz & Paul); spores rusty-melleus rarely subhyaline under the microscope, always perfectly smooth, sometimes apically mucronate or with a callus, mostly with rounded apex, rarely with a slight discontinuity because of the very narrow apical germ pore, mostly without germ pore, with double wall but wall not extremely thick, shape varying according to the species and to specimens, from subreniform-ellipsoid to subamygdaliform-ellipsoid, or ellipsoid to ellipsoid-oblong or somewhat cylindric; hymenophoral trama regular; stipe rather thin, or medium thick, fragile to rather tough but not truly cartilaginous, with a slight to distinct veil, and in many species even subannulate to annulate, without pseudorrhiza, often slightly eccentric and often comparatively short in the wood-inhabiting forms; all hyphae with clamp connections. On the earth and débris of various plants (stems, fruits, fallen leaves), also on dead wood and the cortex of living trees, rarely among mosses.

*Development of the carpophores:* Bivelangiocarpous (Reijnders) in *P. muricata* and *P. granulosa* (and probably all species).

*Area:* Europe, Asia, North and South America, Australia and New Zealand, North and probably also tropical and Southern Africa, in the tropical as well as the temperate regions.

*Limits:* While some authors retain only the subgenus *Phaeomarasmius* in this genus, and Smith & Hesler only the type species, the present author has emended the genus to include aside from *P. erinaceus* also the group called *Flocculina* by Orton (which, if recognized as genus, should be called *Flammulaster*). This group, whether with thick-walled and crystal-incrusted epicuticular cells or thick- or thin-walled with pigment (resinaceous-) incrusted walls represents a perfectly natural generic unit, easily separable from other genera of both Strophariaceae and Cortinariaceae. There exists a series of obviously related forms connecting, both in spore size and thickness of the epicutis hyphal walls and the depth of the epicutis as a whole as well as the covering of the stipe and spore print colors. When the known species of all continents are compared, there is no escape from the conclusion that any attempt at dismemberment - apparently so tempting to some European and North American authors - leads to an artificial solution inasmuch as the abundance of intraparietal and incrusting pigment in the epicutis in all species without spherocysts and even in most of the latter sharply separates *Phaeomarasmius* from *Tubaria*. If the pigment

localization, as emphasized here, produces an obviously natural genus, it cannot be stated that, by using it, we overemphasize its importance artificially. It is another question whether or not *Tubaria* is indeed more intimately linked with the Strophariaceae or the Crepidotaceae. As for that problem, we refer to our discussion of *Tubaria*, p. 681-682.

*Pholiota* subgenus *Hemipholiota* differs constantly in habit and structure of the cuticular layer; not one group or species can be considered similar or related. *Pholiota* sect. *Flavidula* is widely different by its pigments but perhaps somewhat closer to *Phaeomarasmius* than *Hemipholiota*. The rest of the Pholiotas differs by having chryso- or other pleurocystidia and the only group that might be considered related to *Phaeomarasmius* is subgenus *Plocoloma*. Yet, neither section *Flavidula* nor subgenus *Plocoloma* are close enough to be combined with *Phaeomarasmius*. *P. curvipes* has narrow (2-5, some to 9  $\mu\text{m}$ ) basically repent epicuticular hyphae. Section *Flavidula* as originally conceived by Smith & Hesler is a taxon containing unrelated elements (*Pholiota*, *Phaeomarasmius*, *Phaeolepiota*) and cannot be separated from section *Confragosae* in the sense of these authors since at least the European type of the latter is characterized by the same broad, pigment-incrusted, even thickish-walled epicuticular elements as are found in the rest of *Phaeomarasmius* (in NH<sub>4</sub>OH and KOH). On the other hand, Smith & Hesler exclude "many of the species included by Singer (1956) because of the combination of pale colored spores and hygrophanous pilei". It must be remembered, however, that the degree of hygrophanity of the pilei depends a great deal on the density of the covering pulverulence, floccosity or fibrillosity, and the relative density of the pigment of the spores is a purely quantitative character with various degrees which, if emphasized on the generic level, would separate otherwise closely related species - a fact well known to Kühner & Romagnesi (1953) who treated both pale-spored and brown-spored species in the same subgenus.

These pale-spored forms are the expression of a general tendency in various groups of dark-spored agarics which has been treated in chapter I, p. 2. It has caused some mycologists to confuse these forms with *Tubaria* which, however, is clearly different in the structure of the epicutis (a cutis in *Tubaria*, consisting of narrow, basically hyaline hyphae). Other Crepidotaceae differ either in habit or in spore ornamentation; as for *Simocybe*, see there (p. 685).

The tribus of Cortinariaceae have some characters in common with the genus *Phaeomarasmius*, so much so that *Phaeomarasmieae* was once considered a separate tribus of the Cortinariaceae. This was done with some misgivings, and therefore we (Machol & Singer 1972) used a quantitative approach which showed that when the entirety of the characters of *Phaeomarasmius* is taken into consideration, the genus shows more affinity with the Pholiotoideae than the Inocybeae, Cortinarieae and Crepidotaceae even though it appeared that the Crepidotaceae were closer than the Cortinariaceae. This result is to a certain degree in agreement with the views expressed by Smith & Hesler who attached the larger part (viz. all except the type which was considered crepidotaceous) to their broad concept of *Pholiota*. By the same method, we have also determined that *Phaeolepiota* was correctly placed by most taxonomists in the Agaricaceae tribus Cystodermataeae.

*Phaeolepiota*, as it now appears, has a spore wall structure (Pegler & Young 1972) widely different from *Phaeomarasmius* which, added to the spore print color and lack of cheilocystidia, shows that that genus has no close affinities with *Phaeomarasmius*, even the pale-spored forms.

The characteristic epicutis structure of *Phaeomarasmius* is to a certain degree also found in a number of genera now attached to *Inocybe* and Inocybeae. However, even in the acystidiate Inocybes (group of *I. dulcamara*) and in *Alnicola* we have only ectotrophically mycorrhizal fungi; in *Alnicola* the spores are ornamented in a typical Cortinariaceae fashion, and so they are in all brown- or rust-spored genera of the Cortinariaceae with the exception of some smooth-spored Galerinas.

Some species of *Galerina* have smooth spores. The transition from spores with "virtually smooth" spores but showing in chloral hydrate medium after treatment with KOH a marbled surface and a plage, and those which are completely free of exosporial ornamentation is gradual and there is no appreciable hiatus, between them. How do we differentiate between these smooth-spored *Galerinae* and *Phaeomarasmius*? In the first place, these smooth-spored *Galerinae* are either cystidiate and thus different from typical representatives of *Phaeomarasmius*, or else they have no trichodermial epicutis with broad elements and strong pigment incrustation but rather a cutis of gradually thinner and less pigmented thin-filamentous hyphae. Secondly, their habit and affinities are constantly those of the section or subsection of *Galerina* to which they belong, not in the least reminiscent of *Phaeomarasmius*. In the field, at least after an examination with a hand-lens, the experienced collector will rarely have any doubts as to whether a species belongs to *Phaeomarasmius*, and even if he should have doubts, he will hardly ever confuse *Galerina* with *Phaeomarasmius*. Some of the smooth-spored Galerinas have strongly pseudoamyloid spores which is never the case in *Phaeomarasmius*. Others, like *G. nybergii* do not, but these have an epicutis quite different from that of the *Phaeomarasmius*. Besides, *Galerina* is mono-, *Phaeomarasmius* bivelangiocarpous.

*State of knowledge:* The genus *Phaeomarasmius* has been revised and new species have been added by me (1956, 1969) so that by now it may be considered one of the better known genera of the family Strophariaceae. 34 species are here recognized. See Pl. 74.

*Practical importance:* Some species, especially the lignicolous ones, may contribute to the dying of diseased trees including fruit trees but also of shrubs and herbaceous cultivated plants. Their importance may be underestimated in plant pathology at present.

## SPECIES

**Subgenus I. *Phaeomarasmius* (*Rimulincola* Sing. 1948).** Sphaerocysts in the epicutis absent, but epicuticular elements more or less thick-walled, incrusted by crystals or by pigment; spores mostly large: 8-16  $\mu\text{m}$  long; stipe often somewhat eccentric, almost reviving or reviving.

Sect. 1. **PHAEOMARASMIUS** (Characters of the subgenus).

Type species of the subgenus and the section: *P. excentricus* Scherffel.

*P. erinaceus* (Fr.) Kühner (*P. aridus* (Pers.) Sing.); *P. rimulincola* (Rab.) Orton (*P. horizontalis* (Bull. ex St. Amans) Kühner sensu Quél., Kühner non Bull.\*); (*P. excentricus* Scherffel); *P. chiliotrichi* Sing. (*Agaricus exquisitus* Berk. in Hooker, non Vitt.); *P. distans* (Peck) Sing. (*Crepidotus*, Peck); *P. rufolateritius* (Bres.) Sing. (*Crepidotus*, Bres.); *P. alnicola* (Murr.) Sing.

Subgenus II. **Carpophilus** Sing. (1948). Spores generally smaller; epicuticular elements sometimes, all or most, cellular, subisodiametric, or else rather broad and elongated, in chains, and then not thin- to thick-walled. On woody material and other substrata, not eccentric, not reviving.

Type species: *P. carpophilus* (Fr.) Sing.

Sect. 2. **CONFragosi** Sing. (1962). Epicuticular elements in chains of elongated or predominantly elongated hyphous (although rather broad) elements which are always, even in the terminal members, strongly pigment-incrusted.

Type species: *P. confragosus* (Fr.) Sing.

A. Species with a distinct annulus which may be persistent or fugacious:

*P. confragosus* (Fr.) Sing. (*Pholiota*, Karst.); *P. confragosulus* Sing.; *P. pascuus* Sing. ined.

B. Species with indistinct annular zone, or veil not annular:

*P. limulatellus* Sing.; *P. wieslandri* (Fr.) Sing.; *P. subechinatus* (Smith & Hesler) Sing. (*Pholiota*, Smith & Hesler; *Phaeomarsmius suberinaceellus* Sing. ined. "ad int."); *P. limulatus* (Fr. ex Weinm.) Sing. (sensu Joss.; ? *Flammula granulosa* Peck); *P. rostratus* Sing.; *P. eucalypti* (Earle) Sing.; *P. terrigenus* Sing.; *P. nebulosum* Sing.; *P. myrceugenellae* Sing.; *P. confragosuliformis* Sing.; possibly in this section: *Naucoria stagninoides* Orton, and *Naucoria siparia* (Fr.) sensu Lange and sensu Kühner & Romagnesi = *Tubaria ferruginea* Maire ex Kühner. According to Pegler also *P. bowmannii* (Berk.) Pegler. - *Galerina subtruncata* Sm. & Sing. might belong here rather than to *Galerina*.

C. Species with relatively pale colored spores:

*P. fuscomarginatus* Sing.; *P. speireoides* (Romagnesi apud Kühner & Romagnesi ex Kühn. & Rom.) Sing.; *P. malvacearum* Sing. in Sing. & Dig.

Sect. 3. **CARPOPHILI**. Sing.\*\* Epicuticular elements in chains of short-ellipsoid, ovoid or subglobose to globose cells (sphaerocystoid), or at least predominantly so, terminal cells strongly incrusted by pigment or with crystals, or weakly incrusted.

\*Orton has first drawn attention to the fact that Bulliard's plate 324 does not represent this species. It is indeed described as having glabrous, smooth pileus.

\*\*s.n. Epicute cellulifera.

Type species: *P. carpophilus* (Fr.) Sing.

A. Species with normally brownish or brownish ochraceous spores; terminal cells of the trichodermium or epithelium always pigment-incrusted.

*P. granulosus* (Lange) Sing.; *P. floridanus* Sing.; *P. erinaceellus* (Peck) Sing. (*A. detersibilis* Peck non Berk. & Curt.); *P. curcuma* (Berk. & Curt.) Sing.; *P. mucronosporus* Sing. *P. gracilis* (Quél.) Sing. (*Naucoria wieslandri* sensu Kühner & Romagnesi non Fr.); *P. muricatus* (Fr. ex Fr.) Sing. (? *Naucoria mexicana* Murr.); *P. siparius* (Fr.) Sing.; *P. spadiceospinulosus* Sing.; obviously also *Naucoria fulvo-alba* (Berk. & Br.) Sacc.

B. Species with relatively pale colored spores both in print and in KOH mounts; cells of epicutis often scarcely incrusted.

*P. carpophilus* (Fr.) Sing.; *P. gregarius* Sing.; *P. tataricus* Sing. (*Naucoria macrospora* Sing. non Lange); *P. parvuliformis* (Murr.) Sing.; *P. subincarnatus* (Joss. & Kühn.) Sing. also some additional species indicated by Kühner & Romagnesi from Europe.

## CORTINARIACEAE Roze

*Bull. Soc. Bot. Fr.* 23: 51. 1876 (ut *Cortinariées, nom. nud.*); *ibid.*, p. 113; *Heim, Treb. Mus. Ciènc. Nat. Barcelona* 15: 115. 1934.

Type genus: *Cortinarius* Fr.

Syn.: *Hebelomataceae* Locquin, *Flore Myc.* 3: 146. 1977.

*Inocybaceae* Jülich, *Bibl. Mycol.* 85: 374. 1981.

*Cortinariaceae* subfam. *Cortinarioideae* Sing., *Ann. Mycol.* 34: 341. 1936.

*Cortinariaceae* subfam. *Galerinoideae* Sing., *Ann. Mycol.* 34: 342. 1936.

*Agariceae* trib. *Cortinarieae* Fayod (1889), Konr. & Maubl. (1924-37), (both as *Cortinariés*), Imai (1938); *Inocybés*, *Naucoríes* (p.p. Fayod (1889).

*Eu-Derminaceae* Romagnesi, *Rev. Mycol.* 2: 182. 1937 (*nom. nud.*), p.p.

*Phaeotaceae* Romagnesi, *Rev. Mycol.* 2: 178. 1937 (*nom. nud.*) p.p.

Characters: Structure of the epicutis varying from genus to genus but rarely cellular as in the Bolbitiaceae (though sometimes an epithelium in certain species of *Alniconia*) but most frequently either a trichodermium with dermatocystidoid terminal members, or a cutis; hymenophore lamellate; hymenophoral trama definitely regular; spore print brownish argillaceous to bright and rich ferruginous-fulvous rarely porphyry brown to almost white; spores always with compound wall (endosporium and episporium, often ornamented and then marbled to punctate, warty from an exosporial layer\* and with a sometimes rather persistent perispore), mostly (ex-

\*The exosporially ornamented spores of the Cortinariaceae show a very characteristic (for this family) EM structure which has been indicated in the Introduction (p. 85-86). Here the myxosporium appears in the form of an epitunica which in its three substrata (podostratum, mucostratum, and eventually, cerostratum) irregularly gelatinizes forming either warts or by a further development cave-like structures whose cover eventually erodes. The whole ornamentation tends to erode in this case which explains the fact that in some old collections the originally warty spores appear subsMOOTH in light microscopy (Singer, *Persoonia* 2: 2. 1961).

ception: a few species of *Galerina*) without germ pore, but often with a callus, normally binucleate, with open-pore hilum; basidia quite normal in all regards; cystidia often present, more frequently on the edges of the lamellae, more rarely on the sides of the lamellae, and in many species of *Cortinarius* and also in *Rozites* neither with cheilocystidia nor with pleurocystidia; stipe central, more rarely eccentric, lateral or absent; veil present, or absent, if present, frequently cortinoid; context with clamp connections, more rarely without them (some species of *Alnicola*, *Cortinarius* subgenus *Myxacium*, *Phaeocollybia* and one section of *Galerina*). On the earth in woods, more rarely on wood or grass roots, stems, rhizomes of orchids, ferns, on palm leaves, foliage of various plants, charcoal, and in deep moss: often obligatorily endo- or ectomycorrhizal.

**Limits:** The Cortinariaceae "touch" the Strophariaceae on one side, and the Crepidotaceae on the other. However, the Cortinariaceae differ from the Strophariaceae in not combining the essential characters of the latter, viz. absence of mycorrhizal relationships, presence of clamp connections, presence of cheilocystidia, absence of ornamentation on the spores under the light microscope. The Crepidotaceae differ from the Cortinariaceae in being either smooth-spored (and then spores inamyloid and never ectomycorrhizal), or having spore ornamentation of type XI (under the light microscope and of a type quite different from that of the Cortinariaceae when studied in EM sections). The pleurotoid forms of the Crepidotaceae are very different from the only pleurotoid genus of the Cortinariaceae - *Pyrrhoglossum* - both in spore surface markings and spore print color. The spore print in the Crepidotaceae is never bright rusty. Cyphelloid forms do not occur in the Cortinariaceae; their hymenophore is always well developed and distinctly lamellar.

The genera *Ripartites* and *Neopaxillus* differ from the Cortinariaceae by their clitocyboid habit and other characters - anatomical as well as chemical and cytological - and should not be confused with *Cortinarius* where some species with decurrent lamellae occur.

It is not impossible that some species of *Melanomphalia* are still hiding in some genera of Cortinariaceae (especially *Cortinarius* or *Galerina* - little known forms) but the type of spore ornamentation when studied carefully, should eventually reveal their true affinities.

Pale spored forms like *Leucocortinarius* and *Hebelomina* can be mistaken for representatives of the Tricholomataceae but their thicker spore wall and strongly developed cortina, binucleate spores which are either cyanophilic or pseudoamyloid or both, should reveal their affinity with the Cortinariaceae even if the similarity to *Cortinarius* (margined bulb) or *Hebeloma* is overlooked.\*

#### KEY TO THE TRIBUS

A. Spores not ornamented, smooth, not even marbled in KOH or Melzer's reagent, (but sometimes rugulose when seen under the scanning microscope), with even surface or nodulose-gibbous to nodu-

\*With respect to these cases Cléménçon's view at the gradual reduction of the epitunica (p. 85) confirms our disposal of *Leucocortinarius* and *Hebelomina* in the Cortinariaceae and makes them terminal stages of an evolutionary line comparable, by the way, to white-spored Inocybes.

lose-subangular or stellate or tuberculous-spinulose.

- B. Spores very pale colored (pale cream or white). Ectomycorrhizal species (if not cf. *Horakia*, p. 510).
- C. With metuloids (see *Inocybeae*).
  - C. Without metuloids.
    - D. With cheilocystidia; spores pseudoamyloid (or ?amyloid); habit of *Hebeloma* (see *Hebelomatiae*).
    - D. Without cheilocystidia; spores inamyloid; habit of *Cortinarius*, subgenus *Phlegmacium* (see *Cortinarieae*).
- B. Spores strongly pigmented.
- D. Ectomycorrhizal and/or spores with nodulose-gibbous to nodulose-subangular or stellate surface; cheilocystidia usually short, broad, and broadly rounded above; metuloids often present; mycelial cultures difficult to maintain and of limited growth in routine culture media on agar plates; spore print argillaceous brown or tobacco brown, dirty ochraceous fuscous or vaguely rusty-brown
    - Inocybeae*. p. 597
  - D. Not ectomycorrhizal and with even surface (ellipsoid, short ellipsoid, ovoid, oblong, fusoid etc); cheilocystidia usually not clavate to subvesiculose; metuloids none; mycelial cultures easily obtained and maintained in standard culture media on agar plates; spore print more ochraceous brown and often with a stronger rusty tinge (see "E" below).
- A. Spores with an exosporial ornamentation, not nodulose-gibbous to nodulose-subangular or stellate.
- E. Spore print porphyry brown, or more commonly tobacco brown to argillaceous brown and then inamyloid, or cream to white (and then spores pseudoamyloid or amyloid); spores always without a well delimited plage, without a germ pore but often with a well developed callus; habit never pleurotoid; cheilocystidia always present and mostly numerous; if a fleshy pseudorrhiza is present, the spore print is argillaceous brown to tobacco brown; all species obligatorily mycorrhizal except a few atypical forms (which always have clamp connections, strictly tobacco- to argillaceous brown spore print, verrucose spores, no plage, no clapyrate spores and normally occur on burned wood or charcoal).
    - Hebelomatiae*, p. 606
  - E. Spore print with a distinct rusty tinge, or cinnamon to brown-ochraceous, rarely either fuscous brown to tobacco brown or cream to white (and then inamyloid and smooth), never prophyry brown; spores often with a well delimited plage; habit pleurotoid or (more often) not; cheilocystidia present or absent; if a fleshy pseudorrhiza is present, the spores are distinctly ferruginous and no veil is present; mycelium with etotrophic mycorrhiza or without it (and then often lignicolous or bryogenous, more rarely humicolous or carbonicolous, and mostly with bright ferruginous spore print, or else either with plage on the spores and clamp connections in the hyphae or without a plage and no clamp connections on the hyphae, or with a long pseudorrhiza)
    - Cortinarieae*, p. 614

### Tribus *Inocybeae* Fayod ex Sing.

Prodri., Ann. Sc. Nat., Bot. VII. 9: 361. 1889 (*Inocybés*); Singer, Lilloa 22: 524. 1949 (publ. 1951) ex Sing. Nov. Hedw., Beih. 77: 175. 1983.

Type genus: *Inocybe* (Fr.) Fr.

**Characters:** Those of the family; spore print generally tobacco brown to argillaceous brown, e. gr. between "sayal br." and 15 H 12 (M&P), (exceptionally nearly white); spores smooth, and correlated with the presence of metuloids which are not metachromatic in cresyl blue mounts or short clavate-subvesiculose broadly rounded cheilocystidia, pileus often radially fibrillose, never with a well delimited plage; spores often nodulose-lobed to uneven-subangular or stellate, with complex wall (under the light microscope) inamyloid, with an apical callus or without it, not with

a distinct apical pore and never truncate; stipe always central (or only exceptionally slightly eccentric by malformation); veil none or slight, often cortinoid, but also sometimes with an appendiculate or annulate veil or with rests of a universal veil which may be visible as a small volva at the base of the stipe or white appressed thin patches over the pileus; pileus epicutis - a cutis or ixocutis, rarely a trichodermium, not hymeniform, but sometimes some cuticular hyphae bundled together and ascendant or erect to form scales or pustules; stipe frequently with one to three kinds of conspicuous dermatocystidia, but chrysocystidia and metachromatic metuloids absent on the sterile surfaces as well as in the hymenium; pleurocystidia frequently present in the form of non-metachromatic metuloids, but otherwise rather rare or exceptional; cheilocystidia, however, always differentiated; hyphae with clamp connections; all species ectotrophically ectomycorrhizal (obligatorily so).

In this tribus we recognize only one genus:

### 167. INOCYBE (Fr.) Fr.

*Monographia Hym. Suec.* 2: 346. 1863.

*Type species: Agaricus relicinus* Fr.\*

Syn.: *Agaricus* tribus *Inocybe* Fr., *Syst. Mycol.* 1: 254. 1821.

*Astrosporina* Schröter in Cohn, *Kryptog.-fl. Schlesien, Pilze* p. 576. 1889.

*Clypeus* (Britz.) Fayod, *Ann. Sc. Nat. VII.* 9: 562. 1889.

*Agaricus* subgenus *Clypeus* Britz., *Hymen. Südbayern* 3a: 4. 1882 ad int.; 3b (*Nat. Hist. Ver. Augs.*, Ber. 27: 149). 1883.

*Agmocybe* Earle, *Bull. N.Y. Bot. Gard.* 5: 439. 1909.

*Inocibium* Earle, l.c. p. 440.

*Inocybella* Zerova, *Nov. Sist.* p. 117-166. 1974.

*Characters:* Pileus fibrillose, the fibrils arranged radially, often splitting radially and then characteristically rimose, or disintegrating and then irregularly lacerate, often also scaly or squamulose, and sometimes with a pallid fibrillose patch from the volva which is rarely developed enough to show up on the surface of the pileus, the uppermost layer of the pileus consisting of repent or at any rate not palisadic hyphae which are always elongate to filamentous and usually radially arranged, rarely imbedded in a gelatinous mass; dermatocystidia rarely present and then very scattered and about the same shape as those of the lamellae; lamellae adnexed to broadly adnate, often sinuate, usually with paler edge when nearly mature; spore

\*Once it becomes clear that Fries himself raised his tribus *Inocybe* to generic rank and that he did this partly because he was convinced that "Sporae scabrae videntur omnibus Inocybis communes; hac nota ... hanc naturalissimam gregem ... a genuinis Agaricis separo" (Fries 1863), there can be only one conclusion, overlooked or ignored by Donk and Horak and recently by Kühner *viz.* that the type species of the genus *must* be chosen so that it coincides with this character. However, as it turns out, *I. relicina* (Fr.) Quél. is not (as Donk assumed) smooth-spored (see also Moser, *Fung. rar. ic. col.* 7: 42. 1978), and may therefore replace our earlier choices (*I. trechispora*, *I. lanuginosa*). The selection of the lectotype is not fully inconsequential since the infrageneric nomenclature greatly depends on this choice. The separation of *Astrosporina* from *Inocybe* is obviously not only taxonomically unnecessary but nomenclaturally inadmissible.

print about the same color\* as in typical *Hebeloma* and *Alnicola*, never distinctly rusty, rarely almost pallid white (*I. cystidiosa*); spores smooth, i.e. not rough or warty\*\*), but sometimes nodose-subangular (Pl. 17), or even stellate-spinose; phaseoliform-reniform, or almond-shaped, or subellipsoid-elongate, or cylindric, with double wall, without germ pore; cystidia almost always present but in some species restricted to cheilocystidia which are then usually clavate-vesiculose, or else assuming the characters of metuloids, often with thick, somewhat stramineous walls and ampullaceous in many cases, rather large and very conspicuous, and in this case usually also occurring on the sides of the lamellae, the pedicel deep-rooting, the apex often muricate with amorphous (resinous) or crystalline incrustations (the cystidia of the latter type are metuloids of the *Inocybe*-type (Pl. 17, 18); stipe central; often beset with dermatocystidia, mostly pruinose from the dermatocystidia at the apex, but in some species with dermatocystidia (like the metuloids and/or the cheilocystidia) almost all the way downwards to the base, the extent of the cystidiate area depending on the attachment of the cortina to the stipe; the cortina often very abundant, in other cases scanty and fugacious, attached to the apex or to the upper portion of the stipe, or also attached to the base of the stipe and forming the continuation the margin of a bulb (and in this case, the stipe usually pruinose-cystidiate all over), fibrous-fleshy, rarely volvate; the partial veil (cortina) usually continuous with the cuticle of the pileus or adnate to it; context fleshy in the pileus, often with a strong characteristic odor (*Berberis*-flowers, *Corydalis*-root, truffles, camphor, ect.); all hyphae with clamp connections; hymenopodium not gelatinized; one species (*I. sclerotica* Heim) rising from a sclerotium-like (protocarpic?) base.

*Development of the carpophores:* Mostly monovelangiocarpous and pileostipitocarpous, more stipitocarpous in *I. dulcamara*; in some species also bivelangiocarpous (*I. asterospora*, according to Reijnders).

*Area:* Within the ectotrophic-area, except *I. matrisdei* Sing.; *I. hyperythra* Rick, *I. amazoniensis* Sing. & Araujo in Sing. et al., and *I. sclerotica* Heim, but some species introduced in the naturally anectotrophic zones with *Quercus* and *Pinus* plantations.

*Limits:* The limits of this genus are rather easy to draw, and even the beginner will soon be capable to recognize an *Inocybe* in the field. If the microscopical characters are also taken into consideration, the identification of an *Inocybe* as such does not cause any difficulties. The nodulose to lobed, subangular or stellate spores of the subgenus *Inocybe* are almost unique in the agarics and remind one of those of the Thelephorineae. However, the spores of *Cystoagaricus* and, to a greater extent, *Crucispora* and *Horakia*, *Conocybe* sect. *Nodulosporae* have similar shapes; but these genera are easily distinguished by their hymeniform epicutis and/or being amycorrhizal.

\* E. gr. between "Chochin" and "burnt umber" (Maerz & Paul) in *I. relicina* (print 1 year old), and "Raw umber" in *I. lacera* (print fresh), also "Malay" in some species, or Pl. 15, E-12 in *I. geophylla*.

\*\*Under the light microscope; the scanning microscope reveals that some but not all species have entirely or partly verruculose surfaces (cf. Pegler 1972) which is not surprising in view of the probability (demonstrated by me, cf. *Persoonia* 1: 387-389. 1960) that *Inocybe* and *Cortinarius* have a common ancestor.

Some Inocybes have an epicutis which - although more often in form of a cutis than a trichodermium may, by the pigment-incrustation of the elements, remind one of *Phaeomarasmius*. Exceptionally lignicolous representatives of the Dulcamara-stirps may even be misinterpreted as *Phaeomarasmius* since they have no pleurocystidia and even spores. Nevertheless, even these fungi are obligatorily ectomycorrhizal and show the Inocybe-type of cheilocystidia and hyphal arrangement in the cuticular layers; their development is monovelangiocarpous.

Some species of *Inocybe* are viscid or even glutinous, and it may be because of these that *Inocybe* was originally combined with *Hebeloma*. Nevertheless, the distinction is now quite easy as soon as the microscopical characters are known.

**State of knowledge:** The genus has been studied in much detail by several modern authors who have all contributed to the knowledge of a genus enormously rich in species (in those regions where *Cortinarius* is the one single genus with the greatest number of species *Inocybe* usually takes second place). Their work is indispensable for those who attempt to determine the species of *Inocybe*. I wish to name in Europe particularly Heim (1931), Kühner, Kühner & Boursier, Kühner & Romagnesi, Favre, Stangl & Veselský, and Stangl & Enderle, in South America Singer, Singer & Araujo, in North America Kauffman, A.H. Smith, D.A. Stuntz, and in New Zealand and the West Pacific Horak, in Japan T. Hongo. A future monograph will profit particularly by the findings of modern authors such as Robbers, Brady & Tylor (*Lloydia* 27: 192-202. 1964) and Pegler & Young (*Kew Bulletin* 26: 499-537. 1972) whose findings are based on a chemical survey or a survey of scanning microscope studies and are also helpful for the infrageneric taxonomy of *Inocybe*. The species of the *Nothofagus* zone have been studied by Singer, Piterbarg (unpublished), and Horak whereby it is remarkable that in South America thus far only cystidiate (with metuloids) species have been discovered (not counting adventitious species). Restricting the survey below to the species seen and identified by myself, I shall enumerate no more than 94 species, but the world flora is considerably richer judging by the large number of Inocybes collected by me in Central Asia, Eastern North America and other regions scarcely touched by floristic surveys; even in Europe, Furrer, Stangl, Veselský, Bon, and others have still been able to discover new elements of the *Inocybe* flora.

**Practical importance:** Two Inocybes, *I. cutifracta* Petch (tropical Asia) and *I. jura-na* Pat. (Europe) are reported as good edible fungi. Several species cause more or less severe poisoning, especially *I. patouillardii*. The poisonings are of the muscarin type, and a list of the species containing this alkaloid has been compiled by various authors. Brown, Malone, Stuntz & Tyler jr. (*Journ. Pharm. Sc.* 51: 853, 1962) developed a chromatographic technique for the quantitation of muscarin analysis in dried carpophores. These authors deny any significant relationship between the existence and quantity of muscarin and the taxonomic position of the species in *Inocybe*. Detectable quantities of muscarin vary from 0.01% to 0.8% in about 75% of the species tested. Since bio-assay methods revealed considerably larger amounts of active substances (Malone, Robichaud, Tyler & Brady, *Lloydia* 24: 204, 1961), Tyler (Festschr. Kurt Mothes, VEB Gustav Fischer Verl. Jena 1965) concludes reasonably that there must be other muscarine-like agents or potentiators present in some spe-

cies. Psilocybin occurs in *I. aeruginascens*, *corydalina*, *haemacta*, and *tricolor* (Besl & Mack, Z. Myk. 51: 183. 1985; Gartz & Drewitz, ibid. p. 199.

All or almost all Inocybes have potential importance in forestry and forest ecology as mycorrhiza-fungi.

### SPECIES\*

Subgenus I. **Inosperma** Kühn., *Bull. Soc. Linn. Lyon* 49: 412. 1983. Spores not nodulose, angular, or spiny-stellate, but evenly ellipsoid, bean shaped, cylindric, ovoid, and smooth. Metuloids absent.

Type species: *Inocybe calamistrata* (Fr.) Quél.

Sect. 1. **DEPAUPERATAE** Lange (1917) (*Dulcamarae* Heim 1931). Pleurocystidia (metuloids) absent; pileus more or less scaly or tomentose-fibrillose to velutinous; context not reddening.

Type species: *I. delecta* Karst. [= *I. dulcamara* (A. & S. ex Pers.) Kummer].

*I. dulcamara* (A. & S. ex Pers.) Kummer; *I. leucoblema* Kühn.; *I. fuscomarginata* Kühn.; apparently also two annulate species: *I. terrigena* (Fr.) Kühn.; *I. agardhii* (Lund) Orton.

Sect. 2. **RIMOSAE** (Fr.) Quél. (em Heim). Cystidia absent on sides of lamellae; pileus smooth and glabrous, but soon becoming radiately innately fibrillose and rimose; context not reddening, or reddening.

Type species: *I. fastigiata* (Schaeff. ex Fr.) Quél.\*\*

*I. fastigiata* (Schaeff. ex Fr.) Quél.; *I. cookei* Bres.; *I. notodryina* Sing. in Sing. & Araujo; *I. jurana* Pat.\*\*\*; *I. patouillardii* Bres.

Sect. 3. **CERVICOLORES** Kühn. & Romagnesi ex Sing. (1961). Metuloids none; pileus squamulose, squamose, squarrose, or tomentose-fibrillose; context reddening; odor aromatic or fruity or earthy.

Type species: *I. cervicolor* (Pers. ex Pers.) Karst.

*I. bongardii* (Weinm.) Quél.; *I. cervicolor* (Pers. ex Pers.) Karst. (*I. corrubescens* Sing.); *I. calamistrata* (Fr.) Quél.

Note: A special section is probably required for species with non-reddening context and pleuro- and cheilocystidia equal: *I. leptocystis* Atk. (*I. hygrophila* Favre).

Subgenus II. **Inocibium** (Earle) Sing. (1962). Differs from subgenus I in the presence of metuloids on the sides of the lamellae.

\*In the following paragraphs the currently favored infrageneric taxonomy is represented. In this, the spore shape is given maximum importance. The reader is, however, also referred to Heim (1931) who outlined an alternative subdivision of *Inocybe* in 9 sections. This classification is possibly as "natural" or more so than the one here given. It has been compiled in the first and second editions of the present work, but is omitted here because it lacks data on the structure of the covering layer of the stipe.

\*\*This is apparently the *A. rimosus* of many earlier authors.

\*\*\* = *A. adaequatus* and *A. deductus* Britz. which, both, would have priority (cf. Stangl & Bresinsky, Zeitschr. Mykol. 47: 231, 238. 1981).

*Type species: Agaricus lacerus* Fr.

Sect. 4. *LACTIFERAE* Heim (1931). Odor strong, aromatic-fruity; context reddening or becoming pink when bruised; metuloids present.

*Type species: I. pyriodora* (Pers. ex Fr.) Kummer.

*I. pyriodora* (Pers. ex Fr.) Kummer; *I. corydalina* Quél.; *I. tricolor* Kühner.

Sect. 5. (Unnamed). Odor not strong, or else spermatic; context reddening or not; pileus white, lilac, or brownish, and then with red or green discolorations; metuloids present.

*Note:* There is a necessity for a unit on the sectional level, containing *I. geophylla*; however, this unit is at present poorly defined. Lange (1938) has it as stirps *Geophylla*, Kühner & Romagnesi as (2<sup>e</sup>) "groupe"; in the sense of the latter, it may be artificial, but we accept it in this sense for the moment:

*I. geophylla* (Sow. ex Fr.) Kummer; *I. argillacea* (Pers. ex Pers.) Sing.; *I. aeruginascens* Babos; *I. godeyi* Gillet; *I. pudica* Kühn.\*; *I. haemacta* (Berk. & Cooke) Sacc. - In South America: *I. geophylloomorpha* Sing. and *I. subgeophylloomorpha* Sing. (but probably more related to sect. *Splendentes*).

Sect. 6. *LACERAE* (Fr.) Sacc.; (*Fibrillosae* Heim). Odor not fruity-aromatic or context not reddening; carpophore, if naked, without violet or lilac tinge; brown scales not covering the stipe up to the apex, nor is the stipe entirely pruinate, pruina present only at the apex (and even there sometimes indistinct, or missing); metuloids absent from the middle zone of the stipe; cortina where demonstrable connecting the margin of the pileus with the apex of the stipe or with a wide zone covering almost the entire surface of the stipe except for an apical zone which is sometimes covered with extrahymenophoral hymenium, and the extreme base; edge of the lamellae deeper brown than the sides, or not.

*Type species: I. lacera* (Fr.) Kummer.

Kühner & Romagnesi distinguish the following "groups" (or stirpes) which might be recognized as subsections (or even sections) by some future monographer (cf. Stangl & Veselský, *Česká Mykologie* 36: 85. 1982).

1. Pileus brown and scaly, at first with violet tinge at least at the apex of the stipe and/or with deeper brown gill edges. (This stirps corresponds to section *Lilacinae* Heim (1931):

*I. obscura* (Pers. ex Pers.) Gillet; *I. squarrosoamethystina* Sing., and three other European species.

2. Pileus and pigments not as above; stipe not pruinate at all:

*I. lacera* (Fr.) Kummer; *I. tenuicystidiata* Horak, and six other European species; in South America to Mexico: *I. bridgesiana* Sing.; *I. subretipes* Sing.; *I. neuquensis* Sing.; *I. mariluanensis* (Speg.) Sing.; *I. jalapensis* (Murr.) Sing. (Naucoria, Murr.), *I. chilensis* Sing. in Sing. & Moser.

\* = *A. flavidolilacinus* Britz. which would have priority (cf. Stangl & Bresinsky 1981).

3. Pileus and pigments not as in stirps 1; stipe pruinate in upper portion:

*I. tigrina* Heim; *I. queletii* Maire & Konrad, and ten other European and Asiatic, often alpine, species including *I. euthelae* (Bk. & Br.) Quél. sensu Heim p.p., Sing., 1953, non Kühn. & Romagn.; *I. lutescens* Velen. - South American species: *I. erythrobasis* Sing.; *I. semilutescens* Sing. (*I. lutescens* Sing.).

Sect. 7. HYSTRICES Stangl & Veselský (1982). Stipe with brown or whitish recurved scales up to the apex, otherwise like the preceding section.

Type species: *I. hystrix* (Fr.) Karst.

*I. hystrix* (Fr.) Karst.; *I. plocamophora* Sing. in Sing. & Araujo.

Sect. 8. SPLENDENTES Sing. (1953). As sect. 6, but stipe entirely pruinate or at least pruinate from the apex down beyond the middle of the stipe; cortina, where distinct, connecting the margin of the pileus with the base of the stipe which is frequently margined-bulbous.

Type species: *I. splendens* Heim.

1. Species with white stipe, or at least not darkening from below, and not pink, cinnamon, brown-red or russet-fulvous at apex:

*I. splendens* Heim; *I. phaeosticta* Furrer and several other species described by Kühner from Europe including *I. posterula* (Britz.) Sacc. (*I. xanthodisca* Kühn.).

2. Species with russet-fulvous, brown-red, pink or cinnamon stipe, at least at its apex:

*I. scabella* (Fr.) Kummer (sensu Bres.); *I. hirtella* Bres.; *I. friesii* Heim; *I. catalaunica* Sing. (*I. friesii* sensu Malençon (Bertault), and five other European species including *I. kuehneri* Stangl & Veselský (*I. euthelae* (Berk. & Br.) Quél. sensu Kühner & Romagnesi non Sing.); *I. halophila* Heim, and *I. sambucina* (Fr.) Quél. - In South America: *I. gigacystis* Sing.; *I. dissocystis* Sing.; *I. dilutecinnamomea* Sing.; *I. fuscofuscinomea* Sing.; *I. subfuscocinnamomea* Sing.).

3. Species with white or whitish yellow stipe which becomes early fuliginous, olive-fuliginous, olive bister at the base, and finally almost completely darkened:

*I. atripes* Atk.

Subgenus III. **Inocybe** [*Clypeus* (Britz.) Lange 1917]. Spores nodulose, angular spiny-stellate (Pl. 16).

Type species: *A. relicinus* Fr.

Sect. 9. (Unnamed\*). Spores not stellate. Cheilo- and pleurocystiodia both similar and thin-walled, or pleurocystidia absent.

*I. argentea* Sing.; *I. leptophylla* Atk.; *I. acystidiosa* Kauffm.; *I. casimiri* Velen.; obviously also *I. magnifica* Horak and perhaps *I. subfulva* Peck.

Sect. 10. **RUBELLAE** Kühn & Boursier (1932). Characters as in sect. 3, subgenus *Inocibium*.

\*This section should eventually be recognized as a subgenus on equal standing as subgenus I.

*The only species known to belong here is I. bresadolae* Mass.

Sect. 11. *INOCYBE* (*Cortinatae* Kühn. & Boursier 1932). Cortina present, inserted more or less high on the stipe which is therefore fibrillose, woolly, or scaly; stipe generally brownish, at least in its lower portion in age, often bulbous, but not margined, with glabrous or pruinose apex but not pruinose all over; metuloids absent from the middle zone of the stipe; context often inodorous or almost so; pleurocystidia generally well developed but their wall often not strongly thickened.

Type species: *A. relicinus* Fr.

Stirps *Umbrina*\*. [Disc of the pileus not squarrose; spores with few (about 12 or fewer) nodulose papillae.]

*I. pseudoasterospora* Boursier & Kühn.; *I. umbrina* Bres.; *I. transitoria* (Britz.) Sacc. (*I. napi* Lange); *I. homomorpha* Sing.; *I. taxocystis* (Favre) Sing.\*\*; *I. radicata* Peck; *I. acuta* Boudier (*I. umboninota* Peck sensu Lange, Heim); *I. boltonii* Heim\*\*\* (*I. subcarpta* Bours. & Kühn.); *I. variabilima* Speg. [*I. lepidoccephala* Speg.; *I. decipientoides* Peck; *I. astoriana* Murr.; *I. ochraceoscabra* Atk.; *I. globocystis* Velen.; *I. carpta* (Scop. ex Fr.) Kummer sensu Ricken non al.; *Astrosporina lanuginella* Schröter in Cohn (sensu Lange, vix Schröter\*\*\*\*)]; *I. amazoniensis* Sing. & Araujo.

Stirps *Lanuginosa*. [Disc of pileus squarrose; spores with more or less numerous very distinct (mostly 9-17) rarely (in *I. relicina*) only up to eight, sometimes low nodulose papillae].

*I. relicina* (Fr.) Quél. (sensu Moser, Fries, non Quél.); *I. longicystis* Atk.; *I. carelica* Sing. (if not too close to the preceding species); *I. cerasphora* Sing.; *I. ovatocystis* Boursier & Kühn. These species are meant to replace the indeterminable collective species *I. lanuginosa* (Bull. ex Fr.) Kummer, but Orton disagrees with Boursier, Kühner, and Romagnesi, thinking that *I. lanuginosa* is interpretable, and calls *I. ovatocystis*: *I. lanuginosa* (Bull. ex Fr.) Kummer.\*\*\*\*\*

Sect. 12 *CALOSPORAE* Lange (1917). Spores ovoid-globose with 16-19 spinose protuberances or protuberances secondarily spinulose to crested, stipe entirely or almost entirely pruinose; with or without margined bulb at base.

\*Kühner uses the more general term "groupe" which, however, has about the same meaning as stirps in the present case.

\*\*c.n. (= *I. decipientoides* var. *taxocystis* Favre, *Res. Rech. scient. Parc Nat. Suisse* 5: 202. 1955).

\*\*\**A. castaneolamellatus* Britz. is according to Stangl & Bresinsky identical and would have priority over Heim's species.

\*\*\*\*Orton (1960) calls this species *I. lanuginella* (Schröter in Cohn) Konrad & Maubl. but the identity of *I. variabilima* Speg. with *Astrosporina lanuginella* Schröter has not yet been proved satisfactorily. But if type studies should confirm Huijsman's statement (quoted from Enderle & Stangl) that *I. curvipes* is conspecific with *I. variabilima*, the former would have 8 years priority over the latter.

\*\*\*\*\*However, *I. longicystis* Atk. also occurs around Femsjö and might have been *I. lanuginosa* sensu Fr. But according to Stangl & Ederle, all the European species of this stirps are varieties of *I. lunuginosa*, excepting *I. relicina*.

*Type species: I. calospora* Quél. apud. Bres.

1. Species with simple spines on the spores:

*I. calospora* Quél. apud. Bres.; perhaps here the American *I. subfulva* Peck (but without metuloids). Also *I. alnicola* Sing. ined. from Argentine.

2. Species with crested spines on the spores:

*I. hyperythra* Rick.; *I. lasserri* Dennis (unless identical with the preceding species); evidently also *I. multicoronata* A.H. Smith and *I. petchii* Boedijn.

Sect. 13. *PETIGINOSAE* Heim (1931). Cuticle of the pileus consisting of a hypodermium of inflated cells which are brownish, and an epicutis of hyaline filaments which are slender with thick walls; stipe entirely pruinose, pinkish fulvous; base of the stipe not bulbous, and not marginated; spores not stellate.

*Type species: I. petiginosa* (Fr.) Gillet.

*I. petiginosa* (Fr.) Gillet [*I. rufoalba* Pat. & Doass.; *I. scabella* (Fr.) Quél. sensu Schröter in Cohn vix. al.].

Sect. 14. *MARGINATAE* Kühner (1933). Cortina none, or inserted at the base of the stipe which consequently is entirely pruinose; stipe covered with dermatocystidia along its entire length or down to the middle, never fibrillose nor squamulose, usually white, pink, or yellowish, usually (but not always) with a marginate bulb at the base; context not reddening on exposure; cystidia generally with thick walls (Pl. 16-17).

*Type species: I. asterospora* Quél.

*I. paludinella* (Peck) Sacc.; *I. xanthomelas* Boursier & Kühner apud Kühner; *I. mixtilis* (Britz.) Sacc. sensu Kühner; *I. fibrosooides* Kühner; *I. dunensis* Orton; *I. pateracea* Quél. sensu Kühner non Heim sec. Kühner [*I. pseudomixtilis* (Britz.) Sacc.; *I. devulgata* (Britz.) Sacc. (non sensu Sing. which = *I. transitoria*)]; *I. decipiens* Bres.; *I. grammata* Quél. sensu Kühner non Heim (*I. albodisca* Peck); *I. asterospora* Quél.; *I. pseudohiulca* Kühner; *I. oblectabilis* (Britz.) Sacc. (*I. hiulca* var. *major* Bres.); *I. paucigibba* Sing. in Sing. & Moser.

Other South American species of this section: *I. subfibrosooides* Sing.; *I. fuscata* Sing.; *I. mixtiliformis* Sing.; *I. fumosifolia* Speg. - Tropical species: *I. tequendamae* Sing.; *I. matrisdei* Sing.; *I. angustifolia* Horak.

*I. neotropicalis* Sing. in Singer & Araujo is intermediate between sect. 9 and 12, with metuloids on the stipe down to the middle and base not marginate, not bulbous.

#### SPECIES INCERTAE SEDIS

I have not attempted to include all species of *Inocybe* studied by me, such as: *I. aemula* (Britz.) Sacc. (sensu Sing.); *I. caucasica* Sing.; *I. cystidiosa* (A.H. Smith) Sing. [Tricholoma, A.H. Smith\*]; *I. ferruginosa* A.H. Smith; *I. viscosissima* (Fr.)

\*This species is close to *I. geophylla* and differs most spectacularly in white or whitish spore print. Since there are absolutely no other characters separating this species from the Inocybes, I am inclined to think

Sacc.; *I. kauffmanii* A.H. Smith; *I. olympiana* A.H. Smith, and a number of species recently analysed or described by Stuntz or Favre.

The following species described in other genera actually belong to *Inocybe* according to the type studies by the author: *I. praefarinacea* (Murr.) Sing. (*Hebeloma*, Murr.); *I. praevillosa* (Murr.) Sing. (*Lepista*, Murr.); *I. pernivosa* (Murr.) Sing. (*Entoloma*, Murr.); *I. felipponei* (Speg.) Sing. (*Collybia*, Speg.); *I. oregonensis* (Zeller) Sing. (*Naucoria*, Zeller); *I. coloradensis* (Tracy & Earle) Sing. (*Naucoria*, Tracy & Earle).

### Tribus *Hebelomataceae* Romagnesi ex Kühn.

*Bull. Soc. Linn. Lyon* 47: 440. 1978 (Hebelomeae).

Spores mostly argillaceous, rarely porphyry or whitish in print, if whitish - smooth and pseudoamyloid (or amyloid?), otherwise almost constantly and regularly punctate or finely verruculose, mostly ellipsoid to almond shaped or fusoid; cheilocystidia numerous. Ectomycorrhizal, except perhaps in one or two species of *Alniconia*.

Type genus: *Hebeloma* Kummer.

#### KEY TO THE GENERA

- A. Spore print white to pale cinnamon-cream; spores consistently smooth. 169. *Hebelomina*, p. 610
- A. Spore print darker; spores usually ornamented.
  - B. Epicutis strongly developed, mostly as an ixocutis, more rarely an ixotrichodermium, never hymeniform nor epithelial; cheilocystidia present but not narrow with very narrow subacute to acute apex; clamp connections present. 168. *Hebeloma*, p. 606
  - B. Epicutis hymeniform or subhymeniform or epithelial, or else hyphal and poorly developed, never gelatinized but superimposed on a subcutis or hypodermium which contains or consists of swollen elements; cheilocystidia often narrow with very narrow subacute to acute apex; clamp connections present or absent. 170. *Alnicola*, p. 612

### 168. HEBELOMA Kummer

*Führ. Pilzk.* p. 22. 1871.

Type species: *H. fastibile* (Pers. ex Fr.) Kummer.\*

Syn.: *Hebeloma* (Fr.) Quél., *Champ. Jura Vosg.* p. 128. 1871-2.  
*Agaricus* trib. *Hebeloma* Fr., *Syst. Mycol.* 1: 249. 1821.

that there are, in certain species of *Inocybe*, aside from normally pigmented forms others with virtually pigment-less spores, and indeed, I have received from the Pacific Northwest, forms otherwise identical with *I. argillacea* but with stramineous spore print. However, *I. cystidiosa* is obviously an autonomous species, characterized by constantly pigment-less spores in addition to other distinctive characters and occupying a definite area.

\* With regard to the type species see Singer, *Persoonia* 2: 25. 1961.

*Roumegueria* Karst., *Bidr. Finl. Nat. Folk* 32: xxiv. 1879.

*Roumeguerites* Karst., l.c. p. 571 (as correction of *Roumegueria*).

*Hylophila* Quél., *Enchiridian*, p. 98. 1886.

*Myxocybe* Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 361. 1889.

*Picromyces* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 438. 1909.

*Hebelomatis* Earle, l.c., p. 430.

?*Metraria* Cooke & Mass. apud Sacc., *Syll.* 9: 82. 1891.

**Characters:** Pileus viscid; epicutis consisting of strongly gelatinous and very thin filaments forming ixocutis, more rarely an ixotrichodermium, hyaline, the terminal members sometimes dermatocystidoid; hypodermium or subcutis more irregular or subcellular with melleous to rusty incrustations of pigment; lamellae pale argillaceous to pallid at first, later becoming deeper brownish but not bright or deep rusty in age (because of the "clove", "coffee", or "bunny" M & P), rarely prophry brown e. gr. "Verona brown", Ridgway acc. to Smith (1983) color of the spore print), often fimbriate or at least with a whitish edge (because of the large number of cheilocystidia); spores melleous, usually warty rough, usually fusoid to boat shaped, more rarely ellipsoid-oblong or ellipsoid, frequently sub acuminate at both ends, with a callus at the apex but without germ pore, without a plage, and sometimes practically smooth in bisporous forms, acyanophilous (as far as known), inamyloid (but damaged or overaged spores sometimes partially cyanophilous and pseudoamyloid according to Besson & Bruchet 1973, in some species described as pseudoamyloid ("dextrinoid") by Smith 1983); basidia tetrasporous, but bisporous forms not rare; pleurocystidia none; cheilocystidia hyaline, versiform, always distinct, crowded, making the edge of the lamellae heteromorphous; hymenophoral trama regular; stipe rather fleshy to fibrous-fleshy, solid or hollow or stuffed, often pure white, and at least white at the apex of young specimens, never lilac or violet; the apex often squamulose or furfuraceous or pruinose, with cortina or without a distinct veil, sometimes with a distinct membranous veil which assumes the shape of an annulus in mature specimens of at least two species, at times the cortina also taking the shape of an annulus (*H. strophosum*); context inodorous, or more often with a characteristic odor, raphanaceous, of marzipan, chocolate, liqueur, hay, or tea leaves; pseudorrhiza sometimes present; context usually at least partly white; all hyphae with clamp connections. On the earth, on foliage, on fallen needles, rarely on decayed wood or in deep moss or on carbonized particles (old fire places); most or all species ectotropically mycorrhizal with conifers, Fagales, *Tilia*, often with Salicaceae.

**Development of the carpophores:** Monovelangiocarpous and apparently generally stipitocarpous.

**Area:** Almost cosmopolitan but only in the ectotrophic area (but frequent - with *Inocybe*) in the gallery forest (with *Salix*) and the alpine zone (with *Salix* and *Alnus* and *Betula*); rare in the tropics.

**Limits:** *Hebeloma* is intermediate between *Inocybe* and *Alnicola*. Some species have occasionally smooth spores, especially the bisporous forms, and these are then theoretically close to the Inocybes and some Strophariaceae. But the former never combine the macro- and microscopical characters of *Hebeloma* (with regard to cystidia, cheilocystidia and epicutis) and the latter are apparently always bivelangiocarpous and non-mycorrhizal.

There are several small *Naucoria*-like (collybioid) species of *Hebeloma* such as *H. pusillum* Lange and *Hebeloma petrakii* (Hruby) Sing. which were studied thoroughly by the author. These small species might easily be confused with *Alnicola*, especially if anatomical characters such as the structure of the epicutis are neglected by the observer. If in these species the covering layer of the pileus were made up of dermatocystidia or an epithelium or even a thin, non-gelatinized hyphous epicutis above a subcellular subjacent layer they would be inseparable from *Alnicola*. What has been described as *Alnicola dasypus* (Romagnesi), cannot be considered as an *Alnicola* since it has all the characters of *Hebeloma* including the epicutis as described by Romagnesi under the name of *Naucoria dasypus*. This species must be considered as *Hebeloma dasypus* (Romagnesi) Sing. There is no truly viscid species known in *Alnicola* thus far, and none has the epicutis made up of filamentous repent hyphae forming an ixocutis or ixotrichodermium.

Fortunately, the genus *Hebeloma* is characterized by a rather uniform external appearance. As soon as the beginner learns to distinguish genera in the agarics, he will remember the characteristic habit and colors of the Hebelomas, and he will soon, unerringly, identify the Hebelomas in the field, and aside from the few small species, there are rarely doubts as to whether a species belongs in *Hebeloma*. The pinkish-cinnamon to ochraceous cinnamon color fading all the way to white near the margin (a few species are predominantly white), and tending to become deeper and richer reddish brown or fuscous in the center, combined with the dull brownish color of the lamellae and the whitish edges, the characteristic odor of many species, their viscosity and their habitat on the ground, give them away immediately. Only when dealing with incomplete material could any *Hebeloma* be confused with *Corticarius* or vice versa, but a microscopic analysis will always correct any possible error.

As for other families, *Hebeloma* may conceivably be confused with strophariaceous genera. This possibility should be kept in mind especially in cases where almost smooth spores are observed. *Hebeloma evensoniae* Smith & Mitchel in Smith, Evenson & Mitchel is aberrant according to its authors, and with the SEM smooth spores and what appears to be chrysocystidia is according to the description, strophariaceous rather than cortinariaceous.

*State of knowledge:* The only modern monograph available for Europe is that by Buchet, *Bull. Soc. Linn. Lyon* 39: 1-132. 1970 (see also *Bull. Soc. Linn. Lyon* n. special 43: 85-96. 1976) which is very useful but does not contain all European species and almost nothing on the extra-European *Hebeloma*-flora. For North America, we can now add A.H. Smith & al., *The veiled species of Hebeloma in the Western United States*, Ann Arbor, 1983. But numerous species have been described by other authors in the meantime. The species enumerated below represent only a fraction of the species existing.

*Practical importance:* It seems to be quite certain that at least one species of *Hebeloma* is poisonous. Some confusion in the statements on this subject can easily be explained by the fact that those reporting the edibility, or non edibility of Hebelomas, did not always have the same species in mind when using the same specific epithet. The question of *Hebeloma* poisoning could not be solved before the taxonomy of

*Hebeloma* was revised. The poisonous species (containing an ester of crustulinol) is called *H. crustuliniforme* by Ricken and *H. sinapizans* in the following treatment. Many or all species are mycorrhizal and as such of potential importance in forestry: most are obligatorily ectomycorrhizal; some facultatively (cf. also Hacksaylo & Bruchet, *Bull. Torr. Cl.* 99: 17-20. 1972).

Subgenus I. **Porphyrospora** (Konrad & Maubl.) (1948 ut sectio) Sing. Spore print fresh brown with a purple or reddish shade, dehydrated between "auburn" and "English oak" (M. & P.).

Type species: *H. porphyrosporum* Maire.

*H. sarcophyllum* (Peck) Sacc.; *H. porphyrosporum* Maire (unless too close to the preceding species); according to Holland & Pegler also *H. victoriense* Holland & Pegler.\*

Note: The species referable, according to spore print color, to this subgenus may, in America, intergrade with the following subgenera or sections since Smith, Evenson & Michel (1983, p. 15) have found "a gradation of spore color from light clay color to reddish cinnamon to purple brown without a clear line of separation which would be used taxonomically".

Subgenus II. **Myxocybe** (Fayod) Konrad & Maublanc (1924-37). Annulus membranous, well formed and persistent; stipe with pseudorrhiza.

*H. radicosum* (Bull. ex Fr.) Ricken (Pholiota, Kummer; Myxocybe, Fayod).

Subgenus III. **Hebeloma**. Spore print sordid brown ("clove" to "coffee" (M. & P.). Annulus, if present, cortinoid or fugacious and stipe never at the same time distinctly annulate and radicant.

Type species: *H. fastibile* (Pers. ex Fr.) Kummer.

Sect. 1. **HEBELOMA** [*Indusiata* (Fr.) Sacc.]. Veil distinct in young specimens (after primordial state).

Type species: *H. fastibile* (Pers. ex Fr.) Kummer.

*H. strophosum* (Fr.) Sacc.; *H. mesophaeum* (Pers.) Quél.; *H. testaceum* (Batsch ex Fr.) Quél.; *H. fastibile* (Pers. ex Fr.) Kummer; *H. velatum* (Peck) Peck; *H. gregarium* Peck; *H. pascuense* Peck; also obviously several other European and North American species.

Sect. 2. **DENUDATA** (Fr.) Sacc. (1887). Veil generally visible only in the primordia.

Type species: *H. crustuliniforme* (Bull. ex St. Am.) Quél.

*H. sacchariolens* Quél.; *H. fusipes* Bres.; *H. austroamericanum* (Speg.) Sacc. (H.

\*The authors of this species express the opinion (*Trans. Brit. Myc. Soc.* 80: 157-160. 1983) that it is extremely likely that *H. victoriense* corresponds to the spore print conserved at Kew with the type painting of *Metraria insignis*. If the spore print was not later added by Cooke but actually belongs to *Metraria insignis*, *Metraria* would then be a synonym of *Hebeloma*. But Reid (1980) thought that *M. insignis* very closely resembles *A. rosea* Reid. *Metraria* is therefore indicated here as a doubtful synonym of either *Amanita* or *Hebeloma*.

*odoratissimum* (Britz.) Sacc.); *H. gigasporum* Gröger & Zsch.; *H. tomentosum* (Moser) Gröger & Zsch.; *H. anthracophilum* Maire; *H. earlei* Murr.; *H. longicaudum* (Pers. ex Fr.) Kummer; *H. sinapizans* (Paul. ex Fr.) Gillet; *H. edurum* Métrod; *H. crustuliniforme* (Bull. ex St. Amans) Quél.; *H. pusillum* Lange; *H. lugens* (Jungh.) Kummer; *H. hemale* Bres.; *H. australe* Murr.; *H. moseri* Sing.; *H. alpinum* (Favre) Bruchet; *H. vaccinum* Romagnesi; *H. gomezii* Sing. in Sing. & Araujo.

### SPECIES INCERTAE SEDIS

*H. dasypus* (Romagnesi) Sing.; *H. petrakii* (Hruby) Sing.; *H. subcollariatum* (Berk. & Br.) Sacc.

### 169. HEBELOMINA Maire

*Bull. Soc. Hist. Nat. Afr. Nord* 26: 12. 1935.

*Type species: H. domardiana* Maire.

*Characters:* Habit much like that of *Hebeloma*, more or less tricholomatoid; pileus pale colored, somewhat viscid, with an epicutis of repent filamentous hyphae forming a cutis (ixocutis); hypodermium also - a cutis, without distinct membranal or intracellular pigment, but at times a yellowish diffuse color present in hypodermium and gill trama (which is strictly regular, consisting of filamentous hyphae); lamellae rounded-emarginate to adnexed, at the margin subacute to subobtuse (young margin incurved), pallid or eventually with an ochraceous orange flush, 3-4 mm broad; spore print in thick layer not obtained but in thin layer white or whitish; spores under the microscope hyaline, in the herbarium some eventually stramineous, with firm double or triple wall which is rather thick to very thick, with the outermost layer (exo- or perisprium) giving a strong almost amyloid reaction with the Melzer reagent (if not previously hydrolyzed by ammonia), smooth, pseudoamyloid (but moderately strongly so and some spores sometimes remaining inamyloid, "amyloid" according to Maire in the type species), with suprahilar depression, generally with granular contents, fusoid-mucronate to ellipsoid, of medium size or large (7-15  $\mu\text{m}$  long), without germ pore, with the endosporium (at least in *H. microspora*) distinctly metachromatic in cresyl blue mounts; basidia normal in all regards (not excessively long, without carminophilous granulation, generally 4-spored, hyaline); cystidia none, or very inconspicuous cystidioles present; cheilocystidia making the edge of the lamellae heteromorphous, crowded, hyaline, ampullaceous to ventricose-subcapitate, or somewhat constricted underneath a claviform apex, etc., conspicuous; chrysocystidia, metuloids, macrocystidia, none; dermatocystidia present only at the apex of the stipe (in the type species), otherwise absent; hyphae inamyloid, with many clamp connections; stipe equal or subequal, not bulbous, but sometimes slightly thickened towards base, fibrous-fleshy, solid or stuffed, often more or less pruinose at apex, innately or superficially silky or silky-fibrillose below; veil either practically absent, or (in *H. microspora*) well developed, fibrillose, but not leaving an annulus or a volva, pseudorrhiza none; neither pileus

nor stipe nor context distinctly hygrophanous; spores according to Maire binucleate; taste slightly to distinctly bitter; odor of iodoform or raphanaceous. On the ground or attached to small branches in woods. Probably ectomycorrhizal.

*Development of the carpophores:* "Hemiangiocarpous"; in *H. huijsmaniana* according to Huijsman angiocarpous.

*Area:* North Africa and Holland.

*Limits:* Among the pallid-spored genera with firm thickened walls in the spores, this genus differs from all Polyporaceae, Tricholomataceae, and Hygrophoraceae by the behavior of the spores in the Melzer, binucleate spores, and the shape of the spores, structure of their walls, etc. The genus comes closer to the Amanitaceae and Agaricaceae by the binucleate spores but differs from the former in the lamellae which are not free and the hymenophoral trama which is not bilateral. It might be schematically inserted in the Agaricaceae because of the structure of the spores (with metachromatic endosporium in cresyl blue mounts), but differs sharply from the genera with free lamellae because of the attachment of the lamellae and the absence of an annulus, the viscid pileus etc., and from the genera with non-free lamellae in the structure of the velar layers and the covering layers of pileus and stipe. It has, indeed no relatives in that family, and its schematic insertion there would be highly unnatural.

There are spore-albinoes in the Strophariaceae, Cortinariaceae, and pallid-spored genera in the Crepidotaceae, Cortinariaceae, Paxillaceae, and Boletaceae. The structure of the hymenophoral trama as well as the general appearance and the sum of other characters exclude the Crepidotaceae and the Paxillaceae as well as the Boletaceae, so that we are certainly justified in considering only the Strophariaceae and the Cortinariaceae. Certain characters especially of *H. huijsmaniana* seem to point at the strophariaceous origin of the genus, inasmuch as the present author was able to demonstrate a strong pseudoamyloid reaction of the experimentally (McKnight) obtained spore-albinoes in *Psilocybe*, but, on the other hand, these spores of *Psilocybe* were not otherwise similar to those of *Hebelomina* since they showed a somewhat different behavior in iodine solutions (being simply strongly pseudoamyloid) and had a strongly developed broad truncate germ pore. One may still think of a more pholiotoid origin of *Hebelomina*, perhaps from species of *Hemiphloiotia* where fusoid spores and lack of pleurocystidia as well as lignicolous habitat are not uncommon, but the other homologies are rather scarce or far-fetched.

In the Cortinariaceae - where we have eventually decided to place *Hebelomina* - spore albinos exist, as far as we know, in *Inocybe*, but here the cheilocystidia (and in the white-spored forms the metuloids) do not provide any *tertium comparationis*. It must therefore be assumed that, according to our present knowledge, *Hebelomina* is either related to *Cortinarius* and *Leucocortinarius*, or to *Hebeloma*.

Maire has already emphasized the similarity and affinity with *Hebeloma* and expressed this opinion in the generic name. Even *H. huijsmaniana* shows more similarity with *Hebeloma* than with *Cortinarius* or *Leucocortinarius* so that we accept Maire's view for the genus as a whole.

Among the Cortinariaceae, *Hebelomina* differs from all species of most genera in the color of the spores (or rather the lack of pigment), excepting *Leucocortinarius*, but from the latter it differs in veil characters (consistency, attachment - as far as there is a veil at all), in iodine sensitivity of spore walls, and a number of minor characters. *Hebelomina* differs from the white-spored Inocybes in cystidial characters, from pale-spored *Phaeomarasmius* in the structure of the cuticular layers and size, habit, and habitat. *Hebelomina* differs from *Hebeloma* in the smooth, colorless spores. It differs from *Collybia* sect. *Stripedes* in angiocarpy and habit, and apparently its ecology and physiology.

*State of knowledge:* Only two species are known until now, which have been described completely by their respective authors; *H. huijsmaniana* has also been re-studied by the present author thanks to a fragment of the type and drawings sent to him by Huijsman.

*Practical importance:* Unknown.

## SPECIES

*H. domardiana* Maire; *H. huijsmaniana* Sing.\*

### 170. ALNICOLA Kühner

*Contr. Etude d. Hymenomycetes*, p. 175. Paris 1926.

*Type species: Naucloria melinoides* (Bull. ex Fr.) Kummer sensu Kühner.\*\*

*Syn.:* ?*Naucloria* Fayod, *Prodrome, Ann. Sc. Nat.* VII. 9: 357. 1889 non Kummer nec (Fr.) Quél.

*Characters:* Pileus not viscid, squamulose, fibrillose, or glabrous to subglabrous; epicutis not gelatinized, often hymeniform, formed by dermatocystidia or at least neither deep nor in form of an ixocutis, with a subcutis or hypodermium producing apical projections which appear as terminal members of the swollen elements, or the salutis or hypodermium consisting of spherocysts which often form an epithelium or at least contain many swollen almost isodiametric erect hyphal cells intercalated among the filamentous hyphae of a cutis-like structure (cutis heteromerous), or else the spherocysts in chains, forming a trichodermium, or at least some cells of the chains spherocyst-like or vesiculose; spores with a verrucose or finely verruculose-punctate exosporial ornamentation and in every regard much like those of *Hebeloma*, including color of the spore print, usually rather large ( $> 9 \mu\text{m}$ ); cheilocystidia

\*nom. nov. (*H. microspora* Huijsman ex Huijsman, *Persoonia* 9: 485. 1978 non *H. microspora* Huijsman ex C.L. Alesio & U. Nonis, *Micol. Ital.* 6: 19. 1977).

\*\*This species has later been renamed *N. escharoides* (Fr. ex Fr.) Kummer by some mycologists (i.e. sensu Konrad), but the Friesian species has been interpreted differently by Ricken and others with just as much justification and in this case it would be a *Tubaria* rather than an *Alnicola* (see also p. 849). On the other hand, the binomial chosen by Kühner (1926) has traditionally (Höhnel, Kryptogamae Exsiccatae 2209 belongs here) and without contradiction been applied to an *Alnicola*.

present and numerous and often (in sect. *Alnicola*) characteristically narrow and tapering to a subacute or acute apex; pleurocystidia none; hymenophoral trama regular with parallel or interwoven hyphae; basidia normal but often bisporous; stipe central, often elongate and longer than the diameter of the pileus, thin, usually (but not always) pigmented; veil cortina-like but sometimes rather sparse; context fleshy but thin, consisting of hyphae with or without clamp connections. On the ground and on foliage and other debris, rarely on wood, charcoal, frequently under *Alnus*, more rarely *Salix*, and mostly obligatorily ectomycorrhizal.

*Development of the carpophores:* "Hemiangiocarpous" - monovelangiocarpous, stipitocarpous or somewhat pileostipitocarpous.

*Area:* Following the area of *Alnus* through Europe, Asia, Central and South America and besides sparsely represented in Southern South America (Saliceta and wooded zone of Patagonia), but there possibly adventitious.

*Limits:* Easy to delimit in the Cortinariaceae, but see also under *Simocybe*, *Hebeloma*, and *Naucoria* (p. 606-7, 686 and 848).

*State of knowledge:* 13 species are now recognized. Key in *Sydotzia* 30: 206-210. 1977.

*Practical importance:* Where Alni are important forest trees as in South America, the ectomycorrhizal properties of *Alnicola* may have some potential importance for the forester. European alders planted in Chile are generally ectomycorrhizal with European species of *Alnicola* sect. *Alnicola*.

## SPECIES

Sect. 1. *SUBMELINOIDEAE* Sing. (1939). Cheilocystidia usually rather thick, not attenuate or acute at the apex.

*Types species:* *A. submelinoides* Kühner.

*A. mirabilis* (Atk.) Sing. (Galerula, Atk.); *F. salicis* (Orton) Bon; *A. langei* Kühn. in Kühn. & Romagnesi) Sing.; *A. submelinoides* Kühner; *A. inculta* (Peck) Sing. [Galera, Peck; Naucoria celluloderma Orton; Alnicola, Svrcek;? Alnicola alnetorum (Maire in Kühner) Romagnesi]; *A. devia* Sing.; *A. bohemica* (Velen.) Sing. (sensu Orton); possibly *A. lignicola* Sing.

Sect. 2. *ALNICOLA* (*Melinoideae* Sing. 1939). Cheilocystidia narrow, tapering to a subacute or acute apex or broadly rounded and tapering cheilocystidia mixed, the latter predominating in adult caps.

*Type species:* *A. melinoides* (Fr. sensu Ricken) Kühner.

*A. amarescens* (Quél.) Romagnesi (Naucoria, Quél.); *A. luteolofibrillosa* Kühner; *A. suavis* (Bres.) Kühner; *S. scolecina* (Fr.) Romagnesi (sensu Lange) (*A. umbrina* (Maire) Sing.; Tubaria, Maire; Naucoria, Maire non Bres.; Alnicola badia Kühner non subnud. 1926 ex Kühner 1931; Naucoria phaea Kühner & Maire apud Maire; Naucoria spec. Sing. 1929); *A. melinoides* (Fr.) Kühner (Naucoria, Quél. sensu

Kühner 1926, Höhnel, Sing.; *Naucoria escharoides* (Fr. ex Fr.) Kummer sensu Konrad vix Fr., non Ricken, non *Agaricus escharoides* Secri.; Alnicola, Romagnesi); *A. paludosa* (Peck) Sing.; *A. velutina* (Murr.) Sing.; *A. diplocystis* Sing.; apparently also *Naucoria subconspersa* Kühn in Kühner & Romagnesi ex Orton and *A. geraniolens* Courtecuisse.

### Tribus *Cortinarieae* Fayod

*Prodrome*, Ann. Sc. Nat., Bot. VII. 9: 371. 1889 (ut tribus Agaricacearum, Cortinaries); Konr. & Maubl., Icon. Sel. Fung. 6: 122. 1924-37 (item); Ulbrich, Höh. Pilze, p. 258. 1928; Imai. Journ. Fac. Agric. Hook. Imp. Univ. 43: 200. 1938.

Type genus: *Cortinarius* Fr.

Syn.: *Cortinariaceae* subfam. *Cortinarioideae* Sing., Ann. Mycol. 34: 341. 1936.

*Cortinariaceae* subfam. *Galerinoideae* Sing., Ann. Mycol. 34: 342. 1936.

*Cortinariaceae* subfam. *Cortinarioideae* (Sing.) Locqu., Fl. Myc. 3: 146. 1977.

*Cortinariaceae* subfam. *Gymnopiloideae* Locqu., l.c.

*Cortinariaceae* subfam. *Rozitoideae* Locqu., l.c.

*Cortinariaceae* subfam. *Myxacioideae* Locqu., l.c.

*Strophariaceae* trib. *Gymnopileae* Kühn., Bull. Soc. Linn. Lyon 47: 567. 1978.

**Characters:** Those of the family; spore print generally deep ochraceous or brown with a strong rusty component or even bright rusty to orange-rusty, exceptionally whitish or pale cream to ochraceous and then stipe with a margined bulb and connected with ectomycorrhizal mycelium; spores rarely smooth (and then metuloids absent, either without cheilocystidia or not ectomycorrhizal), more frequently ornamented by an exosporial ornamentation which consists of an outer spore layer with cavities and irregularly uneven, usually deeply colored brown in KOH, whereby the spore (according to the thickness of this layer) appears marbled, punctate or verrucose to verrucose-ridged in the light microscope; this exosporial ornamentation often surrounded by a perisprium which may or may not loosen, with an apical callus or without it, but in few species (of *Galerina*) with a narrow, non-truncate germ pore, pseudoamyloid or inamyloid, with or without a plage; stipe central or strongly eccentric to lateral; veil none (but then stipe usually with a pseudorrhiza), or present in form of a cortina, or membranous and forming or not an annulus; sometimes aside from the partial also a membranous outer veil present; cheilocystidia present or absent, but if absent - fungi always ectomycorrhizal; pleurocystidia rarely in form of metuloids and then fungi non-mycorrhizal and metuloids metachromatic in cresyl blue mounts; blue, violet, or lilac intracellular pigments often present, sometimes dominant in species of some groups of both ectotrophically micorrhizal (*Cortinarius*, *Rozites*, *Stephanopus*, *Cuphocybe*) and non-ectomycorrhizal genera (*Gymnopilus*, *Pyrrhoglossum*, *Phaeocollybia*) but seem absent in *Galerina*, *Leucocortinarius*.

### KEY TO THE GENERA

A. Fungi generally forming ectotrophic mycorrhiza with forest trees (or their shrubby or subherbaceous relatives) and difficult to grow (mycelium growing slowly and sometimes not at all in the standard

agar media like potato dextrose agar without vitamine addition); spores constantly with a distinct exosporial ornamentation *and* without a well delimited plage (rarely with a plage and then cheilocystidia absent) unless spore print light cream colored and spores smooth and inamyloid (but then with a margined basal bulb and distinct cortina); cheilocystidia and pleurocystidia both absent, more rarely present; cortina mostly well developed but absent in *Rozites*, *Stephanopus*, and *Cuphocystis*, besides also membranous veils, glutinous veils, even a volva often present (but not necessarily so); clamp connections present, rarely absent (and then stipe usually glutinous).

B. Spores smooth, subhyaline, whitish to light ochraceous in print (mostly pale cream when fresh); cortina and basal bulb present. 175. *Leucocortinarius*, p. 656

B. Spores when mature ornamented (typically by warty or ridged elevations with irregular cavities); the ornamentation mostly a rather deep brown in KOH (on a less strongly pigmented episporial base), not whitish to pale ochraceous in print but rusty brown to dark rusty brown but sometimes almost orange-rusty.

C. Inner veil membranous, both the partial and the universal veil developed and usually light colored, whitish; spores usually with a strong mucro and pseudoamyloid, rather large; hyphae usually amyloid-incrusted. 171. *Rozites*, p. 616

C. Inner veil usually a more or less well developed cortina, rarely the inner veil membranous but then outer membranous veil absent and/or spores different; an outer membranous veil, often pigmented, may also be present, but species with both inner and outer veil membranous are not (yet?) known (if evelate, see "G" below).

D. Anthraquinonic pigments (always endocrocin) abundant; small to medium sized carpophores with yellow, green, orange, yellow-brown or red lamellae and cylindric to slightly clavate stipe. 174. *Dermocybe*, p. 653

D. Not combining these characters.

E. Spores with well delimited plage, viscid pileus and blue or violet pigments.

176. *Stephanopus*, p. 657

E. Spores generally without plage, or not combining the characters indicated above.

F. Outer veil squamulose; cortina absent; spores large (at least 11.2 µm long).

172. *Cuphocystis*, p. 617

F. Not combining these characters.

173. *Cortinarius*, p. 618

A. Fungi not capable of forming obligatory or facultative ectotrophic mycorrhiza but may form endotrophic mycorrhiza; often easy to grow from trama-fragments on standard agar media; with generally distinctly rusty spore print; clamp connections and cortina present or absent; sometimes veil missing except in the primordia; spores with exosporial ornamentation, more rarely without it, often with a suprahilar plage but if plage is absent mostly either without clamp connections or with a distinct pseudorrhiza or with a black reaction with KOH on the surface of the carpophores (in the latter case carpophores most frequently lignicolous, distinctly ornamented, and with bright rusty spores in print); if the tissue cultures grow poorly or extremely slowly in standard agar cultures, veils including cortina poorly developed or none, and habit collybioid; cheilocystidia present.

G. Carpophores collybioid with a generally well developed and conspicuous pseudorrhiza, without any kind of veil in mature fruiting bodies; spores ornamented, without plage.\*

H. Clamp connections present; KOH in pileus immediately dark chestnut and eventually almost black; cheilocystidia ventricose-subcapitate; spores strongly verruculose and pseudoamyloid; pileus and stipe with yellow pigment (see "I" below).

H. Clamp connections present or absent; KOH reaction mostly less strong; cheilocystidia as above or different; spores as above or more weakly ornamented; specimens not combining all the characters indicated above. 179. *Phaeocollybia*, p. 663

G. Carpophores collybioid, mycenoid, rarely somewhat omphaloid, often tricholomatoid, or pleurotoid, with or without veil; rarely and then slightly radicant; spores ornamented or more rarely smooth, with or without plage.

\*Horak (1977) indicates and/or illustrates a well developed plage in some Phaeocollybias (*P. californica*, *mexicana*, *columbiana*, *spoliata*, *fallax*, *viridis*, *attenuata*, *similis*). I have studied the spores of *P. columbiana*, *attenuata*, and *similis* and find these species without a true plage. There may be a different interpretation of the term plage or else the line of loosening of the perispore might have been interpreted as the outline of the often present smooth or weakly ornamented plage area.

- I. If the spores are without plage, they are either completely smooth, or else the absence of a well delimited plage is correlated with absence of clamp connections in both the inflated, firm-walled, and the filamentous thin-walled hyphae of the trama of the carpophore; more frequently the spores have a distinct suprahilar plage which is smooth or subsMOOTH and well delimited; stipe central.  
 (If blue or violet pigments are abundant cf. 180. *Galerina*, p. 666)
1. Spores without plage; hyphae of the trama with clamp connections; habit sometimes pleurotoid (with eccentric to sublateral stipe or with strongly reduced stipe).  
 J. Stipe central or somewhat eccentric (and then spores  $>6 \mu\text{m}$  or exosporial ornamentation projecting  $<1 \mu\text{m}$  beyond the episporium and stipe longer than 4 mm); KOH on the surface of the carpophores staining these brown to black (if not so or spore ornamentation of type XI, compare *Crepidotaceae*).  
 177. *Gymnopilus*, p. 658
- J. Stipe strongly eccentric in mature carpophores, sometimes sublateral or strongly reduced, often short and curved; spores small ( $<6 \mu\text{m}$ ) or if up to  $10.5 \mu\text{m}$  long - heavily ornamented with the ornamentation projecting about  $1 \mu\text{m}$  or else stipe not longer than 4 mm; KOH darkening the spore and pileus surface (if not so, compare *Crepidotus*).  
 178. *Pyrrhoglossum*, p. 662

## 171. ROZITES Karst.

Hattsv.; *Bidr. Finl. Nat. Folk* 32: xx. 1879.

*Type species: R. caperata* (Pers. ex Fr.) Karst.

*Characters:* Pileus with a rather thick but at times discontinuous layer of parallel, filamentous, smooth hyphae without dermatocystidia; hypodermium subcellular (at least in *R. caperata*), but no hymeniform layer in the cuticle of the pileus; spore print rather light to medium bright rusty colored near "Argus brown" (Ridgway) or "Sudan br." (M & P); spores melleous, punctate or verruculose with exosporial ochraceous brownish warts, broadly amygdaliform and generally rather voluminous, without plage and without germ pore but more or less mucronate with a callus, pseudoamyloid; basidia normal tetrasporous; cystidia none; cheilocystidia none or very scattered and inconstant; hymenophoral trama regular; stipe central, without pseudorrhiza, without a margined bulb, without a cortina but with a membranous annular veil and in addition with a more or less developed membranous external veil in the lower part of the stipe; hyphae typically amyloid-incrusted, with clamp connections; carpophores rather large and fleshy (more or less tricholomatoid), growing on forest soil, ectotrophically mycorrhizal; hymenophore develops HCN (at least in the type species).

*Development of the carpophores:* Probably bivelangiocarpous and hymenopileocarpous (Reijnders).

*Area:* With certainty known only from the ectotroph area of the Northern Hemisphere (but in the sense of Moser widespread).

*Limits:* This genus is well delimited from other genera of the Cortinariaceae by several good characters but it should be noted that the pseudoamyloidity and to a certain degree even the ornamentation of the spores are not well preserved in very old dried material.

Moser (1953) distinguishes a section *Australiensis* from a section *Rozites* (Capera-

tae). The former has a glutinous covering and no amyloid incrustation on the hyphae (Cléménçon 1971). I believe that the section *Australiensis* is too close to certain groups of *Cortinarius*, at least judging by the material I have studied personally, although the veil characters seem to be those of *Rozites*. The position of this section remains doubtful. Horak recently transferred the type species (*R. australiensis* Cleland & Cheel) to *Cortinarius*.

*Rozites* is often similar to *Descolea* in habit and spore characters but differs in less ochraceous spore print and the absence of a hymeniform epicutis.

*Rozites gongylophora* is agaricaceous (see under *Leucoagaricus*).

*State of knowledge:* This author is familiar with only two species corresponding closely to the generic diagnosis.

*Practical importance:* *Rozites* belongs to the less specialized ectotroph-formers, and may, precisely for that reason, become important in forestry; *R. caperata* is also widely known as a good, edible species. The same observations are also valid for Horak's (1981) New Zealand species.

## SPECIES

*R. caperata* (Pers. ex Fr.) Karst.; *R. emodensis* (Berk.) Moser. - According to Horak (*Sydowia* 34: 94-108. 1981) also *R. similis* Horak & Taylor; *R. fusipes* Horak & Taylor; *R. rugosiceps* Horak & Taylor; *R. pallida* Horak & Taylor; *R. castanella* Horak & Taylor; *R. collariata* (Horak & Moser) Horak; *R. ochraceoazurea* (Horak in Horak & Moser) Horak (Thaxterogaster, Horak in Horak & Moser; *Cortinarius*, Horak & Moser in Moser & Horak); *R. sarmienti* (Speg.) Horak (see also under *Cortinarius sarmienti* Speg. p. 626); *R. gamundiae* Horak; *R. neocaledonica* Horak; *R. meleagris* Horak & Taylor.

*Note:* Since in the descriptions of the above species Horak does not mention the amyloidity of the hyphal incrustation or the pseudoamyloidity of the spores, the precise position of these species within *Rozites* and/or the final delimitation of the genus with regard to *Cuphocybe*, *Cortinarius*, and *Stephanopus* requires further studies.

## 172. CUPHOCYBE Heim

*Rev. Myc.* 16: 8. 1951.

*Type species:* *C. olivacea* Heim.

*Characters:* Pileus and stipe covered with usually appressed scales, or fibrils the stipe also sometimes with a belt-like zone near the base, the scales of velar origin, but without an apical or mediane annulus and without cortina; spores large (above 11.2  $\mu\text{m}$  long), ovoid-ellipsoid, more rarely somewhat amygdaliform, verrucose (in EM sections of H. Cléménçon typical of the *Cortinarius*-type), without plage, with-

out plage, without germ pore, binucleate, sometimes irregularly constricted or with dorsal suprahilar protuberance, ferruginous-brown to melleous-ochraceous (as in *Rozites*) in KOH, spore print ferruginous-brown; basidia normal; cystidia none; cheilocystidia absent or very inconspicuous and rare; hyphae with clamp connections; hymenophoral trama regular; lamellae often with eroded edge and/or transversely pallid-striped (under a lens) because of splitting of the hymenium in the direction of the hymenophoral hyphae. Otherwise much like *Cortinarius* and *Rozites*. Apparently ectomycorrhizal with Fagaceae.

*Development of the carpophores:* "Hemiangiocarpous" but not known in detail.

*Area:* New Zealand, New Caledonia, New Guinea.

*Limits:* This genus has nothing to do with *Descolea* from which it differs in spore shape and absence of a hymeniform epicutis as well as other macro- and microscopical characters and the apparent connection with ectomycorrhizal Fagaceae roots, as pointed out by Horak (1983), but not confirmed for *Descolea*. The comparison with *Descolea* resulted from an exchange of preliminary notes on both *Descolea* and *Cuphocybe* by Roger Heim and myself whereby the possible identity of the two genera was discussed but later rejected. I personally am familiar only with the type species of *Cuphocybe* and agree with Horak that it belongs in the Cortinariaceae, close to *Cortinarius*. The differences between this genus and *Rozites* in the larger sense are restricted to veil characters. It is possible that some species of *Rozites*, in spite of being annulate, might eventually appear too close to *Cuphocybe* when chemical characters are better known. For the time being, *Cuphocybe* should be characterized by the absence of an annulus, by pigmented veil fibrils or scales, and by non-mucronate spore apex, as well as by the lack of a cortina.

*State of knowledge:* Satisfactory for the type species, with three others obviously congeneric (see Horak, *Nova Hedw. Beih.* 43: 193-200. 1973; *Sydotia* 33: 60-62. 1980).

*Practical importance:* At present none, but possibly useful in forestry as ectotroph formers.

## SPECIES

*C. olivacea* Heim; according to Heim also *C. alborosea* Heim; according to Horak also *C. ferruginea* Horak and *C. phaeomyxa* Horak ("phaomyxa").

## 173. CORTINARIUS Fr.

*Genera Hymenomycetum*, p. 7. 1836.

by M. Moser\*

*Type species:* *C. violaceus*-(L. ex Fr.) Fr.

\*I am very pleased to acknowledge the kindness of my friend and colleague, Dr. Meinhard Moser who consented to revise the chapter on this difficult and large genus for me, inasmuch as my own experience on this genus is rather limited. R.S.

- Syn.: Cortinaria* (Pers. ex Fr.) S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 627. 1821.  
*Hydrocybe* (Fr.) Wünsche, *Pilze* p. 87, 119. 1877.  
*Telamonia* (Fr.) Wünsche, *Pilze* p. 87, 122. 1877.  
*Myxacium* Kummer, *Führ. Pilzk.* p. 22. 1871.  
*Phlegmacium* (Fr.) Wünsche, *Pilze* p. 87, 128. 1877.  
*Cortinarius* trib. *Hydrocybe* Fr., *Epicrisis* p. 303. 1838 (nom. nud.); subgenus *Hydrocybe* Rabenh. (sub. *Agaricus*), *Deutsche Krypt.* p. 488. 1844.  
*Agaricus* trib. *Telamonia* Fr., *Syst. Mycol.* 1: 210. 1821.  
*Agaricus* trib. *Myxacium* Fr. l.c. p. 247.  
*Agaricus* trib. *Phlegmacium* Fr., l.c. p. 226; subgenus, Rabenh. (sub. *Agaricus*), *Deutsche Krypt.* p. 498. 1844.  
*Inoloma* (Fr.) Wünsche, *Pilze* p. 87, 126. 1877.  
*Agaricus* trib. *Inoloma* Fr. *Syst. Mycol.* 1: 216. 1821; subgenus, Laudon (1829).  
*Gymnocybe* Karst., *Hattsv.*, *Bidr. Finl. Nat. Folk* 32: xxvii. 1897, non Fr. (1827).\*  
*Sphaerotrichys* Fayod, *Prodr. Ann. Sc. Nat.*, Bot. VII 9: 374. 1889.  
*Gomphos* Kuntze, *Rev. Gen. Pl.* 2: 385. 1891, non *Gomphus* S.F. Gray (1821).  
*Bulbophodium* Earle, *Bull. N.Y. Bot. Gard.* 5: 441. 1909.  
*Hydrocybium* Earle, l.c. p. 440.  
*Meliderma* Velen., *České Houby*, p. 399. 1920.  
*Leucopus* Kummer, *Führ. Pilzk.* p. 22, 85. 1871 (not validly published).  
*Raphanozon* Kummer, l.c. (not validly published).  
*Cereicium* Locqu., *Fl. Myc.* 3: 146. 1977.\*\*  
*Cyanicum* Locqu., l.c.  
*Hygramaricum* Locqu., l.c.  
*Hygromyxacium* Locqu., l.c.  
*Myxopholis* Locqu., l.c.  
*Sarcoloma* Locqu., l.c.  
*Squamaphlegma* Locqu., l.c.  
*?Cystocybe* Velen., *České Houby* p. 495. 1920.  
*?Weinzettlia* Velen. l.c. p. 514. 1921 (see also p. 677).  
*?Quercella* Velen., *České Houby* p. 495. 1921 (see also p. 675).

*Characters:* Habit very variable, from mycenoid to collybioid, clitocyboid, tricholomatoid to nearly pluteoid; pileus glutinous, viscid, opimous, or hygrophanous, or at the same time viscid and hygrophanous, or else dry, i.e. neither hygrophanous nor viscid and then squamose, squamulose, rimose, fibrillose, silky, or glabrous, sometimes even tomentose or innately floccose; lamellae subfree to decurrent, narrow to broad, with various colors in young specimens (according to species, sections or stirpes), later becoming more richly colored in the color of the spore print, characteristic even in mature well dried material, deep rusty and somewhat dusty in most cases; spores under the light microscope (KOH) rusty ochre to melleous, more or less strongly warty-rough, but never actually smooth, without loosening peri-

\* Donk (1962) differed from Singer & Smith (1946) in selecting *G. abrupta* rather than *G. weinmannii* as type species for reasons I consider invalid. However, I agree now with Donk and Horak for a reason not mentioned by them, viz. the fact that Lange, *Dansk Bot. Ark.* 5: 14-15. 1928, appears to have selected by inference *G. abrupta* for what he thought to be the same as his section *Gymnotae* ("Gymnocybe Karst.") although his interpretation of *G. abrupta* is different from that of Karsten (really = *Gymnopilus*, sect. *Gymnopilus*). If then *G. abrupta* (Fr.) Sacc. sensu Karst. is the type of *Gymnocybe*, it would follow that *Gymnocybe* is a synonym of *Cortinarius* in view of Horak's type studies (1968, p. 714): "On the basis of the scarce characteristics still demonstrable microscopically, we believe that *Flammula abrupta* sensu Karst. represents a species of the stirps *Cortinarius gentilis* Fr. (Spores 6.5-7.5 (5-5.5 µm, verrucose)" (our translation). R.S.

\*\* This and the following six synonyms were added to Moser's manuscript later. R.S.

sporium (not calyptrate), without suprahilar plage\* and without a germ pore but often with a distinct callus; consisting of at least an episporium and an endosporium, the ornamentation perhaps of exosporial origin, a perisporium also often evident, globose, subglobose, ellipsoid, ellipsoid-oblong, lemon-shaped, cylindric-oblong amygdaliform, etc.; basidia 4-spored, in the Northern Hemisphere rarely, in the Southern often 2-spored; cystidia rarely present on the sides of the lamellae,\*\* more often on the edges (cheilocystidia); hymenophoral trama regular; stipe central, with an inner veil and an outer veil, the former generally in form of cortina but in some groups forming a membranous annulus instead, the outer veil varying from very fugacious to persistently belt-like (annular to peronate) on the lower portion of the stipe, of fibrillose to woolly consistency, but in some groups forming a distinct membranous volva, the outer veil often entirely mucilaginous, the inner veil attached to lower part of the stipe or more often to the upper part, later often characteristically dusty from the rusty spores, sometimes with several belts (formed by the outer veil - as in *Telamonia* spp.) and these variable in pigmentation; a purple to vinaceous or bluish to violet color (intracellular pigment) often present; not or rarely combining hygrophanous pileus with abundant anthraquinonic pigments. Most species forming obligatory ectomycorrhiza with Pinaceae, Fagales, Salicales, Tiliaceae, Caesalpiniaceae, some genera of Myrtaceae\*\*\* and Rhamnaceae; several species apparently forming also endomycorrhizae in Ericaceae (Vaccinioideae), especially in subgenus *Telamonia*.

*Development of the carpophores:* "Hemiangiocarpous"; bivelangiocarpous or in some cases rather monovelangiocarpous, pileocarpous, pileotipitocarpous, in some species (e.gr. *C. pholideus*) rather stipitocarpous\*\*\*\* (Reijnders).\*\*\*\*\*

\*According to verbal communications from Dr. J.E. Wright and Dr. A.H. Smith, the former has observed a slight plage in the spores of *Cortinarius violaceus*. However, all species with a habit comparable (and colors comparable) with the habit (and colors) existing in the genus *Galerina*, have spores without plage. For a EM section of the spores see Pl. 53c. R.S.

\*\*And then with refringent coarsely granular contents (*C. pseudocrassus*) or yellow granular incrustation (*C. subtortus*), see Moser, *Pilz. Mitt.* 4, pl. D, 197-199.

\*\*\*These are *Eucalyptus* and *Leptospermum*, now often separated, in my opinion correctly, as family Leptospermaceae. - Some Amazonian species are connected with Sapotaceae. R.S.

\*\*\*\*An interesting observation by Moser (1960) seems to be significant in this regard. He has established that there are two main types represented in the subgenus *Phlegmacium* of *Cortinarius* — which in itself would not be surprising since this, according to Douglas's data (1916), is also the case in other subgenera of *Cortinarius*. These two main types - type A and type B which would perhaps roughly correspond to the pileotipitocarpous and the stipitocarpous type respectively - have been observed by Moser in one case (*Cortinarius pseudosulphureus*) to coexist in a single species, whereby type A was observed in nature whereas type B was observed in pure cultures. Moser wonders "whether these types are not a function of the habitat or controlled by some other factors (temperature and humidity, nutrition, etc). On the other hand we must ask ourselves whether type B is degenerative and derived or to be considered primitive". It is my impression that the volva-development favors an earlier development of the pileus. If so, it would follow that the stipitocarpous development is more primitive if the volva is considered derived (a recent acquisition). However, if controlled by environmental factors, the succession pattern may easily be, alone together with the factors indicated by Moser, influenced by light intensity. This, at least, would follow from such data of experimental embryology as cited and given by Taber (in Ainsworth & Sussman, 2, 1966). R.S.

\*\*\*\*\*It is recommended to study the compilation of data by Reijnders (1979). R.S.

**Area:** Coincides with the area of the ectotroph-dominated communities. Very rich in species in the temperate zone of North America, Europe and Asia; also in the mountains of the subtropical and tropical regions as far as the mycorrhizal partners occur; also in the temperate zones of the Southern Hemisphere especially with *Nothofagus* and *Leptospermaceae*; outside these areas very rarely found in association with cicatrizer-mycorrhiza and in plantations.

**Limits:** Most, especially the larger carpophores are easily recognized, even by the beginner; and if the generic diagnosis is carefully checked, few species will present difficulties in generic determination as long as all characters are properly stated. There is a possibility of confusing some of the smaller *Cortinarii* with *Galerina*, *Dermocybe*, and *Melanomphalia*. As for *Dermocybe*, see there; as for *Galerina* and *Melanomphalia*, it should be taken into consideration that both these genera are non-mycorrhizal and that they do not have a constant well delimited plage on the inner side of the spore base if the hyphae are clampless or if the ornamentation is of type XI. They are also distinguishable from *Cortinarius* by their cystidial characters. *Gymnopilus* has been confused with *Cortinarius* in the past. But this genus is likewise never ectomycorrhizal and combines dry pileus with the presence of cheilocystidia.

**State of knowledge:** Many species of *Cortinarius* have been studied in some detail by Henry, Moser, Kühner & Romagnesi, Orton and A.H. Smith. These authors are now beginning to publish keys and regional monographs for certain or all groups, especially in *Phlegmacium*. In spite of some excellent work done by several authors in the past, some, especially "exotic", species are still insufficiently defined or the interpretations are at variance. These papers show that many of the older species are collective though they may not have been collective in Fries's personal concept. As for the macroscopical characters, Fries's *Monographia* is still one of the important sources for North European species. Ricken and Velenovský gave excellent accounts with indications of spore characters, and - where observed - cystidia. In addition, microscopical characters were indicated by Kauffman (in *North American Flora*, l.c.) and by A.H. Smith in various papers, illustrated with excellent photographs. Chemical characters appear to be of great assistance in the identification and classification of the *Cortinarii* as is shown by Henry's, Bataille's, Moser's, and Orton's papers as well as in the treatment by Kühner & Romagnesi. A careful study of the various types of pigments and a more detailed study of the cortical layers of both pileus and stipe, and other anatomical characters, including the size and shape of the cheilocystidia in such groups as *Telamonia* has also materially helped to solve some of the difficulties encountered in the study of the *Cortinarii*, as had been suggested previously by Singer in the first edition of the present work, as well as by Kühner (*Bull. Soc. Nat. Oyonnax* 3: 1-8. 1949).

Ecological characters, particularly mycorrhizal specialization, also provide important data for the specific differentiation.

The genus *Cortinarius* with its several hundred species, takes gradually but unmistakably in the fungus-flora of Europe the place *Rubus* and *Hieracium* are occupying in the phanerogamic flora although there is no indication that their sexuality or speciation is analogous to that of these genera. The great variety of forms and

groups is evidently a consequence of adaptation to various mycorrhizal hosts and climatic conditions inside the temperate zones and the mountains, the subarctic and subantarctic as well as the subtropical zone. 627 species are recognized in the enumeration below.

**Practical importance:** Perhaps all species of *Phlegmacium* and the largest part of the other species are connected with forest trees, shrubs and subherbaceous birches and willows, by mycorrhiza. For the purposes of forestry - mainly artificial development of mycorrhiza - only *Phlegmacium* has been used until now since in this case pure cultures are achieved more easily than generally in *Cortinarius*.

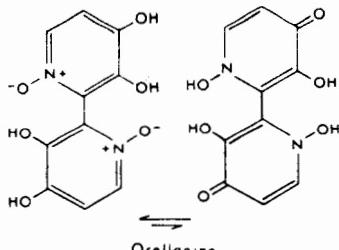
The largest part of the species belonging to *Phlegmacium*, *Myxarium*, *Sericeocybe* and *Hydrocybe* is probably edible. *C. orellanus* and *C. speciosissimus* are deadly poisonous. They contain "orellanine"\*. The symptoms of the poisoning are said to appear after 3-14 days.

*C. venenosus* Kawamura is also indicated as poisonous (this species apparently belongs in *Cortinarius*). Alkaloids are said to occur in *C. cyanites*.

## SPECIES

Subgenus **Phlegmacium** (Fr.) Fr. Habit tricholomatoid, fleshy, pileus hygrophanous or not, glutinous to dry and even tomentose (and then in the context yellowish brown to yellow with alkalis). Lamellae subfree to decurrent, but mostly sinuate-adnate, whitish argillaceous, to bright blue, yellow, greenish or olive. Stipe equal, clavate, or marginate-bulbous, often brightly colored, dry, rarely viscid. External veil present, but in mature specimens often absent or remaining as pruina or fibrillosity on the surface of the pileus, more rarely as volva-like formation on the basis of the stipe. Uppermost layer of cuticle of pileus often mucilaginous, consisting of relatively narrow hyphae of 2-8-(10)  $\mu\text{m}$ . Hyphae always clamped, but distribution of clamps often unequal in the carpophore. Spores ellipsoid, ovoid, fusoid or amygdaliform, lemon-shaped or subglobose, subsMOOTH to very coarsely verrucose. Cheilocystidia in some species observed, pleurocystidia very rare. Blue and violet

\*According to Schumacher & Høiland (*Arch. Toxicol.* 53: 87-106, 1983) orellanine is a bipyridine:



This structure had been proposed first by Antkowiak & Gessner (*Tetrahedron Lett.* 21: 1931-1934, 1979). Another poisoning factor may be cortinarin A, B, and C, a cyclopeptide-like group (cf. Bresinsky-Besl 1985, p. 51). R.S.

pigments plasmatic, the others intercellular or in oleiferous hyphae. Taste mild or bitter.

Type species: *C. saginus* (Fr.) Fr.

Sect. 1. *PHLEGMACIUM*. Pileus with whitish, ochraceous, orange-ffulvous or darker brownish pigments. Lamellae whitish, argillaceous, argillaceous brownish (rarely somewhat violet-lilac). Stipe white, yellowish, brownish, sometimes somewhat bluish or lilac at the apex, with or without margined bulb. Veil strongly to weakly developed, white, flesh-brownish or somewhat violet-tinged (never yellow or yellowish brown). Context never bright colored. Alkali with context a variable dull brown (never reddish brown or yellow discoloring), or reaction negative. Spores amygdaliform, narrowly fusoid, rarely subglobose or almost lemon-shaped, sub-smooth to strongly ornamented. Brown and yellow pigments epimembranal-intercellular, blue pigments if present plasmatic.

Type species: *C. saginus* (Fr.) Fr.

Subsect. *Multiformes* Henry ex Moser (1961). Pileus whitish, brown, yellow, orange-ffulvous. Lamellae whitish, argillaceous or very pale bluish. Stipe generally margined-bulbous, more rarely clavate. Veil weakly developed, or else with a violet shade, or (rarely) white.

Type species: *C. multiformis* (Pers. ex Secr.) Fr.

Stirps *Allutus*. [Pileus orange brown to red brown, yellow brown, mostly with a covering reminding one of a pruina, sometimes hygrophanous, not innately fibrillose or scarcely so. Lamellae argillaceous or whitish. Stipe white, later brass colored, base indistinctly or distinctly margined. Spores less than 10 µm long (rarely slightly over 10 µm long). Sulfoformol coloring the context slightly greenish to greenish blue].

*C. allutus* Fr. (*Agaricus luteus* bulbiger Secr.); *C. lundellii* (Moser) Moser (*Phlegmacium*, Moser); *C. subhygrophanicus* (Moser) Moser (*Phlegmacium*, Moser; *C. allutus* sensu Lange non Fr.).

Stirps *Multiformis*. (Pileus ochraceous brown to yellowish brown or orange brown, pruinose or with fibrillose veil remnants, more or less innately fibrillose, 20-200 mm broad. Lamellae whitish to argillaceous. Spores mostly larger than 10 µm. No reaction with sulfoformol. Otherwise like the preceding stirps).

*C. multiformis* (Fr. ex Secr.) Fr.; *C. luteoimmarginatus* Henry; *C. ochropallidus* Henry; *C. talus* Fr.; *C. gracilior* [(J. Schäffer ex) Moser] [*Phlegmacium* (J. Schäffer ex) Moser].

Stirps *Inflatipes*. (Pileus ochraceous, yellow-brown, brown, lamellae whitish, argillaceous to rusty yellow, stipe whitish with bulbous, sometimes margined base; spores elliptic to slightly amygdaliform. Differing from the preceding stirpes by the lack of any reaction with KOH, acids, phenol, sulfoformol etc. Under *Nothofagus* in South America.)

*C. xylochroma* Horak; *C. cholooides* Horak; *C. bulbosomustellinus* Moser & Horak;

*C. unguicularis* Horak & Moser; *C. luteomelleus* Moser; *C. melleus* Moser & Horak; *C. inflatipes* Moser; *C. tricholomoides* Moser; *C. albobrunneus* Moser.

Stirps *Napus*. [Thick-fleshy species with generally broad stipe. Pileus ochraceous brown, chestnut, buff (color or paper carton), orange brown or even yellowish. Lamellae argillaceous. Spores amygdaliform.]

*C. napus* Fr.; *C. pseudonapus* [(Henry ex) Moser] Moser [Phlegmacium, (Henry ex) Moser]; *C. corrosus* Fr.; *C. saporatus* Britz.; *C. elegantulus* (Moser) Moser (Phlegmacium, Moser); *C. argillopallidus* J. Schäffer; *C. lutulentus* J. Schäffer; *C. aurantiacus* Moser; *C. fulminoides* (Moser) (Phlegmacium, Moser).

Stirps *Paxilloides*. (Pileus with sordid brown, ochraceous to reddish brown tinge, center soon depressed. Lamellae argillaceous. Spores amygdaloid to lemon-shaped.)

*C. paxilloides* (Moser) Moser (Phlegmacium, Moser); *C. calyculatus* Moser.

Stirps *Pallidolamellata*s. (Pileus yellow, yellow-brown, brown, lamellae very pale, whitish, pallid, pale brown or argillaceous, stipe fusoid to cylindric or slightly clavate, white whitish. Under *Nothofagus* in South America.)

*C. pallidolamellatus* Horak & Moser; *C. argenteohygrophanus* Moser; *C. umbrinocarneus* Moser; *C. austroserarius* Moser; *C. simplex* Horak; *C. cucumis* Horak; *C. paucicolor* Horak.

Stirps *Argillohygrophanicus*. (Pileus whitish, ochraceous, ivory to pallid argillaceous, often strongly hygrophanous; lamellae pale argillaceous; stipe clavate, cylindric; spores generally less than 11-12  $\mu\text{m}$ .)

*C. argillohygrophanicus* Moser & Horak; *C. spodoleucus* Moser; *C. perpallidus* Moser & Horak; *C. alboochraceus* Moser.

Stirps *Sebaceus*. (Pileus ochraceous yellow to fulvous brown, margin often covered by the veil, center sometimes pruinate. Lamellae argillaceous. Stipe white, sericeous, sometimes hirsute-sheathed when young, base at times with violet veil remainders, with or without margined bulb. Spores fusoid, narrow, or amygdaliform.)

*C. sebaceus* Fr.; *C. corruscans* Fr.; *C. variegatus* Bres.; *C. roseolimbatus* (Secr.) J. Schäffer.

Stirps *Calceolati*. (Species with white, ochraceous to violaceous-pinkish universal veil, with ochraceous flesh-brown, cocoa-brown or brown pileus, with variegated or pruinate appearance, lamellae whitish, pallid to argillaceous, stipe with or without margined bulb. Under *Nothofagus* in South America.)

*C. sagatus* Moser; *C. roseocalceolatus* Horak & Moser; *C. truncatoides* Moser; *C. saccharatus* Moser with var. *bulbosus* Moser; *C. ochraceocinctus* Moser; *C. crassoides* Moser; *C. nothocollinitus* Moser.

Stirps *Lustratus*. (Pileus and stipe white. Stipe equal or clavate. Spores ovoid-ellipsoid.)

*C. lustratus* Fr.

Stirps *Virgineus*. (Pileus chalky white, silky, stipe cylindric to clavate, spores amygdaliform to almost lemon-shaped, 8-11  $\mu\text{m}$ . Under *Nothofagus* in South America.)

*C. darwinii* Speg.; *C. virgineus* Horak & Moser.

Stirps *Microspermus*. [Small species with ochraceous, argillaceous or orange brownish pileus and with clavate or equal stipe; spores small (4-8.5  $\mu\text{m}$  long).]

*C. microspermus* Lange; *C. compar* (Weinm.) Fr.; *C. vespertinus* (Fr.) Fr.

Stirps *Sublubricus*. (Species with the habit reminiscent of *Pholiota lenta*, with gilvous colors and strong glutinosity. Lamellae whitish to pale argillaceous.)

*C. sublubricus* (J. Schäffer apud Moser ex Moser) Moser (*Phlegmacium*, Moser); *C. joannae* Henry.

Stirps *Rapaceus*. [Pileus and stipe whitish, cream, ivory color at times becoming fulvous when old. Stipe with margined bulb (sometimes there is a bluish tinge at the apex of the stipe and in the lamellae). Spores amygdaliform.]

*C. rapaceus* Fr. with var. *luridus* Moser & Horak. *C. amarescens* (Moser ex Moser) Moser; *C. albidus* Peck; *C. leucophanes* Karst.; *C. caroviolaceus* Orton.

Stirps *Cystidiorapaceus*. (Pileus and stipe white to ivory, stipe clavate to margined-bulbous, spores large (11-17.5  $\mu\text{m}$ ); cheilocystidia present, clavate. Under *Nothofagus* in South America.)

*C. tarnensis* Speg.; *C. cystidiorapaceus* Moser; *C. crystallophorus* Moser.

Stirps *Sulphureomyceliatus*. (Pileus ochraceous to umber or sepia, stipe cylindric or with margined bulb, base with yellow mycelium; lamellae pallid to argillaceous. Under *Nothofagus* in South America.)

*C. sulphureomyceliatus* Moser & Horak; *C. gracilipes* Moser.

Stirps *Ocellatus*. (Small species with yellow to brownish pileus with remarkably darker disc region, lamellae argillaceous, stipe cylindric to clavate, whitish, spores elliptic to amygdaliform. Under *Nothofagus* in South America.)

*C. ocellatus* Horak & Moser; *C. discophaeus* Moser; *C. psammopodiooides* Horak.

Stirps *Tumidipes*. (Similar to the subgenus *Telamonia*, with brown pileus, pale to dark brown lamellae, white to brownish stipe, the latter cylindric, clavate, bulbous or margined, and glutinous, non-hygrophanous pileus; spores sublimoniform to limoniform. Under *Nothofagus* in South America.)

*C. tumidipes* Moser; *C. acerbus* Moser & Horak; *C. furnaceus* Moser; *C. dactylochrous* Moser; *C. exaltatus* Horak; *C. sciurodes* Moser & Horak.

*Note:* The position of the stirps is uncertain and it is maintained in the subsection and section on a temporary basis.

Subsect. *Phlegmacium* Moser (1961). Pileus yellow to brown. Stipe clavate or equal,

belted-sheathed by a white or flesh-brown (not yellowish brown!) veil. Spores subglobose, fusoid, amygdaliform, or lemon-shaped.

Type species: *C. saginus* (Fr.) Fr.

Stirps *Saginus*. (Spores subglobose. Pileus yellow, yellow-brown. Stipe thick and robust with white veil.)

*C. saginus* (Fr.) Fr.

Stirps *Claricolor*. (Spores more or less fusoid.)

*C. claricolor* (Fr.) Fr. with var. *claricolor*, var. *turmalis* (Fr.) Moser [*C. turmalis* (Fr.) Fr. and several other varieties]; *C. subclaricolor* (Moser) Orton.

Stirps *Perizonium*. (Pileus yellow to brown; stipe clavate to cylindric, with woolly to submembranaceous universal veil forming white to yellowish belts; lamellae pallid; spores elliptic to amygdaliform. Under *Nothofagus* in South America.)

*C. sarmienti* Speg.; *C. perizonium* Horak; *C. pseudotriumphans* Moser; *C. austroclaricolor* Moser & Horak; *C. pseudoclaricolor* Horak & Moser; *C. squamipes* Horak.

Stirps *Trechisporus*. (Similar to the preceding stirps, but stipe more fusoid, radicant, and veil nearly membranous; spores elliptic to amygdaliform, strongly verrucose. Under *Nothofagus* in South America.)

*C. trechisporus* Horak.

Stirps *Xiphidipus*. (Species with white, yellow to brown pileus, with whitish, argillaceous or brown lamellae and white to brownish stipe which tapers downward usually into a long pseudorrhiza; spores elliptical to amygdaliform. Under *Nothofagus* and *Eucalyptus* in South America, Australia and New Zealand.)

*C. xiphidipus* Moser & Horak; *C. terebrinus* Horak & Moser; *C. effundens* Moser, Horak & Sing.; *C. pugionipes* Moser; *C. cervinus* Moser & Horak; *C. longicaudus* Moser; *C. radicatus* Clel.; *C. mustellinus* Horak & Moser; *C. austroturmalis* Moser & Horak; *C. myxoclaricolor* Moser.

Stirps *Fraudulosus*. (Pileus ochraceous brown, flesh-brown, ferruginous brown or chestnut. Lamellae ochraceous to lilac. Stipe with a white to flesh-brownish veil. Spores amygdaliform to lemon-shaped.)

*C. fraudulosus* Britz.; *C. affinis* Allescher; *C. rufoalbus* Kühner; *C. fluryi* (Moser) Moser (*Phlegmacium*, Moser).

Sect. 2. *TRIUMPHANTES* ad int. (*Cliduchii* Fr. 1836, p.p.). Universal veil yellow, yellow-brown, to olive brown or grayish brown, and pileus similarly colored. Stipe clavate or equal. Spores amygdaliform.

Type species: *C. triumphans* Fr.

Stirps *Triumphans*. (Carpophores with yellow or yellow-brown colors. Veil mostly forming belt-like, often woolly zones at least in the typical forms.)

*C. triumphans* Fr.; *C. crocolitus* Quél.; *C. subtriumphans* Henry.

Stirps *Vitellinopes*. (Color ochraceous yellow, olive-ocher, olive-brown. Velar zones only at base of stipe, membranous-appressed.)

*C. vitellinopes* (Secr.) Schröter; *C. cephalixus* (Secr.) Fr.; *C. papulosus* Fr.

Sect. 3. *CALOCHROI* Moser (1961). Pileus whitish, ochraceous, yellow to brown or orange-reddish, more rarely with olive or greenish, rarely with violet tinges. Lamellae pale lilac to deep violet or blue. Stipe white, yellowish ochraceous, bluish, lilac, more rarely greenish, dry but in South American species sometimes glutinous, with margined or obtusely rounded bulb. Alkalies on pileus surface or on context brown or red. Spores amygdaliform to subglobose. Pigment of cuticle epimembranous-intercellular (except if violet), that of the lamellae plasmatic.

Type species: *C. calochrous* (Pers. ex Fr.) Fr.

Subsect. *Calochroi* Moser (nom. nud.). Pileus whitish, ochraceous, yellow, yellow-brown, violet. Alkalies on cuticle of pileus red-brown, ink-red, pink, violet brown, or negative.

Type species: *C. calochrous* (Pers. ex Fr.) Fr.

Stirps *Spectabilis*. (Pileus whitish, ivory. Lamellae bluish, lilac, violet. Stipe with margined bulb. Alkalies on surface of pileus ink-red, to red brown. Spores amygdaliform.)

*C. spectabilis* Moser; *C. rickenianus* Maire; *C. parvus* Henry; perhaps also *C. aleuroiosmus* Maire.

Stirps *Dibaphus*. (Pileus lilac, violet, orange-ferruginous-brownish. Lamellae when young with a violet shade or lilac. Veil violet. Alkalies on context mostly pink to red, often also on the cuticle pink to violet. Context often bitterish. Spores amygdaliform, more than 10 µm long.)

*C. dibaphus* Fr. with var. *dibaphus* and var. *nemorosus* Henry; *C. suaveolens* Bat. & Joachum; *C. arcuatorum* Henry; *C. fulvoincarnatus* Joachim.

Stirps *Calochrous*. [Species of medium to small size and ochraceous, lemon yellow or tawny (lion skin yellow) or olive shaded pileus, with brown, reddish brown to red alkali reaction on cuticle. Lamellae lilac to pinkish violet. Spores amygdaliform.]

*C. calochrous* (Pers. ex Fr.) Fr.; *C. leochrous* J. Schäffer; *C. platypus* (Moser) Moser (*Phlegmacium*, Moser).

Stirps *Arquatus*. (As previous stirps, but larger. Spores amygdaliform to subglobose.)

*C. arquatus* Fr.; *C. subarquatus* (Moser ex) Moser (*Phlegmacium*, Moser); *C. caesiocortinatus* J. Schäffer; *C. pansa* Fr., *C. cyanophyllus* Henry; *C. citrinolilacinus* (Moser) Moser (*Phlegmacium*, Moser).

Stirps *Trachyphloeus*. (Showing all the main characteristics of the subsection but with very strongly verrucose, amygdaliform to lemon-shaped spores. KOH-reactions unknown. Under *Nothofagus* in South America.)

*C. trachyphloeus* Moser & Horak.\*

Stirps *Rhodophyllus*. (Species with yellow pileus and stipe; stipe clavate or with margined bulb, glutinous, lamellae pink; spores amygdaliform, verrucose. Under *Nothofagus* in South America.)

*C. rhodophyllus* Moser & Horak.

Subsect. *Glaucopodes* Konrad & Maubl. ex Moser (1961). Pileus with olive, grayish brown, umber brown or fulvous, rarely violet shades, sometimes even with greenish colors. Lamellae blue, violet (exceptionally argillaceous). Stipe bluish, violet, or greenish tinted. Alkalies on cuticle umber to red brown, never red. Spores amygdaliform.

Type species: *C. glaucopus* (Schäff. ex Fr.) Fr.

Stirps *Elotus*. (Pileus with olive colored immixtures, basic color ochraceous brown, fulvous-brown. Lamellae whitish blue, lilac, argillaceous, wax-yellow-grayish. Stipe whitish, violet shaded, or blue-green. Spores amygdaliform, 10-15  $\mu\text{m}$  long.)

*C. elotus* Fr.; *C. pseudoglaucus* (J. Schäffer apud Moser ex Moser) Moser (Phlegmacium, Moser); *C. violaceolimbatus* Moser (Phlegmacium pinetorum Moser ex Moser; C., Moser non Kauffman), *C. alnobetulae* Kühn.

Stirps *Glaucopus*. (Pileus ochraceous-yellow, orange-yellow, fulvous, or olive-brown, mostly strongly innately fibrillose, often on greenish ground. Lamellae bluish or greenish, silky-shining. Bulb at times poorly differentiated. Spores amygdaliform, ellipsoid.)

*C. glaucopus* (Schäff. ex Fr.) Fr.; *C. magicus* Eichh. ap. Moser; *C. pistorius* J. Schäffer.

Stirps *Fulvoochrascens*. (Pileus grayish brown, often darker fuscous spotted, rarely with bluish tinge on surface of pileus. Lamellae and stipe blue, bluish violet. Spores amygdaliform.)

*C. fulvoochrascens* Henry (*C. fuscomaculatus* J. Schäffer; *C. caerulescens* Fr. non Secr.) with several varieties; *C. avellaneocaeruleus* (Moser) Moser (Phlegmacium, Moser).

Stirps *Amoenolens*. (Pileus pallid to olivaceous-ochraceous. Lamellae whitish lilac to deep violet blue. Stipe concolorous with lamellae. Bulb more or less rounded and with ocher tinged veil zone. Spores amygdaliform.)

*C. amoenolens* Henry ex Orton; *C. subumbilicatus* Henry.

Stirps *Stephanopus*. (Pileus bluish to grayish green to olivaceous; lamellae lilac to blue, stipe indistinctly margined-bulbous, blue to lilac, with traces of a universal veil; spores coarsely verrucose, amygdaliform to lemon-shaped. Under *Nothofagus* in South America.)

\*Considered to belong to *Stephanopus* by Horak (1979). R.S.

*C. stephanopus* Moser & Horak.

Sect. 4. *PERMAGNIFICI* Moser. Pileus and stipe bright orange, yellow orange, orange-ocher; lamellae deep violet-blue; stipe  $\pm$  fusoid-bulbous; spores obovate to subamygdaliform, slightly verrucose. Under *Nothofagus* in South America.

Type and only species: *C. permagnificus* Horak.

Sect. 5. *CAERULESCENTES* Henry ex Moser (1961). Pileus at least in youth and on margin bluish, violet, lilac, purplish lilac or cuticle somehow brown and alkali reaction on context yellow or brown with yellowish outer zone. Lamellae blue, violet, argillaceous to whitish. Stipe bluish to pallid or brownish. Margined bulb differentiated, or not. Not showing purple spots where pressed or touched. Blue and violet pigments plasmatic.

Type species: *C. caerulescens* (Schaeffer ex Secr.) Fr. ss. Konrad & Maublanc, Moser.

Subsect. *Caerulescentini* Moser. Cuticle of pileus bluish, violet, lilac, bluish gray, silver gray, ochraceous or ochraceous brown discoloring. Lamellae bluish or bluish gray, purplish pink, violet, very rarely whitish or argillaceous pallid. Stipe always with margined bulb or at least with rounded bulb, often margined by a white or ochre-pallid veil. Akalis on context brownish, or negative. Spores amygdaliform.

Type species: Same as in section.

*C. volvatus* A.H. Smith; *C. caesiostamineus* Henry; *C. caesiogriseus* J. Schäffer in Moser ex Moser; *C. sodagnitus* Henry; *C. aureopulverulentus* Moser; *C. dionysae* Henry; *C. caesiocanescens* Moser; *C. foetens* (Moser) Moser (Phlegmacium, Moser); *C. boudieri* Henry; *C. caerulescentium* Henry; *C. arcifolius* Henry, *C. mairei* (Moser) Orton (nom. nud.); *C. sphagnophilus* Peck; *C. caerulescens* (Schaeff. ex Secr.) Fr. (sensu Konrad & Maublanc, Moser and Fries); *C. caesio-cyaneus* Britz.

Subsect. *Cumatiles* Moser (1961). Pileus with blue, violet, or vinaceous-red colors. Lamellae argillaceous-whitish, argillaceous brown, exceptionally violet (not in the type varieties). Stipe whitish, more rarely violet; veil violet, bluish, or ochraceous. Base with margined bulb or without it. Spores relatively narrow and mostly somewhat fusoid but up to 16  $\mu\text{m}$  long and longer.

Type species: *C. cumatilis* Fr.

*C. cumatilis* Fr.; *C. praestans* (Cordier) Sacc.; *C. durissimus* Moser.

Subsect. *Lavendulenses* Moser. Pileus pale violet, whitish-lilac to brownish; stipe clavate, whitish to pale violet; lamellae lilac to brown; context only turning dirty brownish or unchanging with KOH. Under *Nothofagus* and *Eucalyptus* in Australia and South America.

Type species: *C. lavendulensis* Clel.

*C. lavendulensis* Clel.; *C. lilacinofulvus* Clel.; *C. vinaceolamellatus* Clel.; *C. imbecillis* Moser; *C. lazoi* Moser.

Subsect. *Variecolores* Konrad & Maubl. ex Moser. Pileus violet, fulvous, cork color, viscid to almost dry and then tomentose. Lamellae violet to argillaceous and whitish. Stipe violet, brownish or whitish. Context with ammonia and KOH mostly yellow or with yellow outer zone, or yellowish brown. Odor often like dust, or fruity.

Type species: *C. variecolor* (Pers. ex Fr.) Fr.

Stirps *Variecolor*. (Lamellae and stipe violet, sometimes pileus also so colored. Stipe clavate, rarely with margined bulb.)

*C. variecolor* (Pers. ex Fr.) Fr.; *C. nemorensis* (Fr.) Lange; *C. largus* Fr.; *C. livido-violaceus* Henry; *C. spadiceus* Fr.; *C. spadicellus* (Moser) Moser (Phlegmacium, Moser); *C. muricinus* Fr. (apparently here in spite of dry pileus).

Stirps *Varius*. (Pileus fulvous crust-brown. Lamellae violet. Stipe white, clavate. Context with alkalis chrome yellow.)

*C. varius* (Schaeff. ex Fr.) Fr.

Stirps *Latus*. [Carpophore without violet colors (at the most, young lamellae violet). Stipe without a margined bulb. Alkali reaction bright yellow.]

*C. latus* (Pers. ex Fr.) Fr.; *C. inamoenus* (Favre apud Moser) Moser (Phlegmacium, Favre apud Moser); *C. badiolatus* (Moser) Moser (Phlegmacium, Moser); *C. schaefferi* Moser (nom. nud.; Phlegmacium schaefferianum Moser, nom. nud.).

Stirps *Balteatus*. (Pileus brown, perhaps violet on margin, not much viscid or quite dry and tomentose. Lamellae argillaceous-pallid to brown. Stipe whitish, brownish, equal or clavate. Veil whitish or violet. Spores amygdaliform. Alkali reaction yellowish brown or brown, with yellow outer zone.)

*C. balteatus* (Fr. ex Fr.\* Fr.; *C. subbalteatus* Kühn.; *C. balteatocumatis* Henry ex Orton; *C. latobalteatus* (J. Schäffer ex Moser) Moser (Phlegmacium, Moser); *C. hysginus* (Moser) Moser (Phlegmacium, Moser); *C. crassus* Fr.; *C. pseudocrassus* Josserand ex Orton\*\*; *C. balteatoalbus* Henry.

Sect. 6. *SCAURI* Fr. (1936) [*Meliderma* (Velen.) Beck 1922 ut sect. g. *Dermini*; *Phlegmacium* sect. *Laeticolores* Moser]. Small to medium sized species, some even large, with bright colors on pileus, stipe, and lamellae (yellow, green, red, violet, etc.). If the pileus is blue or violet, surface where pressed or touched staining purplish on the stipe and lamellae (which are in this case likewise bluish), also staining like stipe. Stipe with margined bulb, or if simply clavate, carpophore greenish yellow, or yellow, or stipe staining purple.

Type species: *C. scaurus* (Fr. ex Fr.) Fr.

Subsect. *Purpurascentes* Kühner & Romagnesi ex Moser (1961). Context with Lugol or other iodine solutions vinaceous red, with thallium solutions vinaceous red to vinaceous brown. Species with blue, violet, or green colors on lamellae and stipe.

Type species: *C. scaurus* (Fr. ex Fr.) Fr.

\**Syst. Mycol.* 1: 225. 1821; *A. balteatus* Secr. 2: 40. 1833 = *Rhodocybe truncata* (Schaeff. ex Fr.) Sing.

\*\*According to Orton (1960) this species is placed in subgenus *Sericocybe*. R.S.

Stirps *Purpurascens*. (With blue or violet colors on stipe and lamellae and turning purple where pressed or touched.)

*C. purpurascens* Fr. ex Fr.; *C. subpurpurascens* (Batsch ex) Fr.; *C. occidentalis* A.H. Smith; *C. porphyropus* (A. & S. ex) Fr.; *C. subporphyropus* Pilát.

Stirps *Scaurus*. (Lamellae and stipe green-blue, green, or if violet not turning purple where pressed or touched.)

*C. scaurus* (Fr. ex Fr.) Fr.; *C. herpeticus* Fr. with var. *herpeticus* and var. *polychrous* (Henry) Moser; *C. metapolychrous* Moser; *C. subscaurus* (Moser) Moser; *C. parksianus* A.H. Smith; *C. codinae* Maire; *C. virentophyllus* Kauffm.

Subsect. *Orichalcei* Kühner & Romagnesi ex Moser (1961). Habit of carpophores similar to habit of those of the preceding subsection; with margined to indistinct bulb. Colors of carpophores yellow, fulvous, reddish, violet, green (violet colors only if green or yellow colors also present). Lamellae yellow or green. Alkalies with context showing bright color reactions: red, red-brown, green, or salmoneous. Spores amygdaliform.

Type species: *C. orichalceus* (Batsch ex Secr.) Fr.

Stirps *Orichalceus*. (Pileus with brown, fulvous, greenish, violet, purple tinge. Lamellae yellow, green, greenish yellow. Stipe mostly concolorous with lamellae, mostly distinctly margined-bulbous. Alkalies with context either at first turning green, or red to purplish vinaceous).

*C. orichalceus* (Batsch ex Secr.) Fr.; *C. prasinus* (Schaeff. ex Pers.) Fr. (here sensu Konrad & Maubl.); *C. rufoolivaceus* (Pers. ex Fr.) Fr.; *C. odorifer* Britz.; *C. glaucescens* (J. Schäffer apud Moser) Moser (Phlegmacium, J. Schäffer apud Moser); *C. glaucoprasinus* (Moser) Moser (Phlegmacium, Moser).

Stirps *Aureoturbinatus*. (Carpophores with dull to bright yellow colors, on lamellae and stipe; pileus besides often fulvous; stipe at times somewhat greenish. Context white, only yellowish in peripheral parts, or somewhat violet shaded.)

*C. claroflavus* Henry; *C. sulfurinus* Quél.; *C. flavopallidus* (Moser) Moser (Phlegmacium, Moser); *C. aureofulvus* Moser; *C. auroturbinatus* (Secr.) Lange; *C. cedrorum* Maire.

Stirps *Flavovirens*. (Pileus with greenish or olivaceous colors; lamellae and stipe yellow, or greenish yellow. Context in internal portion white.)

*C. flavovirens* Henry; *C. odoratus* (Joguet) Moser [*C. prasinus* var. *odoratus* Joguet; Phlegmacium *odoratum* (Joguet) Moser].

Stirps *Splendens*. (Pileus with yellow or green colors. Context brightly yellow, lamellae and stipe also bright yellow.)

*C. atrovirens* Kalchbr.; *C. splendens* Henry; *C. pseudosulphureus* Henry ex Orton; *C. vitellinus* Moser (*C. majusculus* Kühner).

Subsect. *Percomes* Konr. & Maubl. ex Moser (1961). Pileus yellow or green or partly or entirely ochraceous brown to umber. Lamellae mostly concolorous with

the stipe, yellow, yellowish green, exceptionally argillaceous. Stipe with margined bulb or without it. Context whitish to yellow. Alkalies often reacting purple red. Spores amygdaliform.

*Type species: C. percomis* Fr.

Stirps *Nanceiensis*. (Universal veil brown or brownish violet.)

*C. nanceiensis* Maire; *C. citrinoolivaceus* Moser.

Stirps *Percomis*. (Universal veil yellowish, ochraceous, greenish, generally not visible on the fully developed carpophore.)

*C. percomis* Fr.; *C. guttatus* R. Henry; *C. russeoides* Moser; *C. russeus* Henry (nom. nud.).

Subsect. *Panchroi* Moser. Pileus, lamellae and stipe with bright colors, pale to dark yellow, greenish, lilac, blue; stipe cylindric to clavate-bulbous, never margined, with alkalies either becoming orange, or only a brownish reaction, or negative (no reaction); spores elliptical to amygdaliform. Under *Eucalyptus* and *Nothofagus* in South America and Australia.

*Type species: C. panchrous* Horak.

Stirps *Panchrous*. (With KOH no reaction, or only a dirty brownish one.)

*C. panchrous* Horak; *C. aganochrous* Horak; *C. rancidus* Moser; *C. coarctatus*, *C. luteoecaeruleus* Moser; *C. ochraceocaeruleus* Moser; *C. oleaginus* Clel. & Harris; *C. austroevernius* Clel. & Cheel.

Stirps *Viridulifolius*. (Pileus and stipe yellow, lamellae with a slight green hue; spores amygdaliform, verrucose; KOH on pileus and context orange to orange-brown.)

*C. viridulifolius* Moser.

Stirps *Flammuloides*. (Pileus and stipe with bright chrome to golden yellow colors, lamellae pale yellowish; stipe cylindric to clavate; spores amygdaliform to lemon-shaped.)

*C. flammuloides* Horak & Moser; *C. obrusseus* Horak.

Sect. 7. *AMARESCENTES* Moser (1961). Lamellae with some olive shade, light to dark grayish olive or fuliginous olive. Taste bitter or at least slightly bitter. Spores subglobose to ovoid-ellipsoid.

*Type species: C. infractus* (Pers. ex Fr.) Fr.

Stirps *Infractus*. (Lamellae dark fuliginous-olive. Context with AgNO<sub>3</sub>, immediately black. Spores subglobose. Taste strongly bitter.)

*C. infractus* (Pers. ex Fr.) Fr.; *C. rotundisporus* Cleland.

Stirps *Amurceus*. (Lamellae grayish green to olive green. No reaction with AgNO<sub>3</sub>. Taste slightly bitterish. Partly with cystidia.)

*C. amurceus* Fr., *C. subtortus* (Pers. ex Fr.) Fr. [C. *jasmineus* (Secr.) Fr.].

Sect. 8. *FULVI* Moser (1961). Stout species with straw, wax-, or orange yellow lamellae. Pileus yellowish brown, orange brown, yellow-fulvous or more rarely oliveaceous. Base of stipe with margined bulb (or bulb at least marginated-truncate), sometimes with well developed volva. Spores often rather large, amygdaliform to lemon-shaped.

*Type species: C. elegantior* Fr. ex Fr.

Subsect. *Elegantiores* Moser. Larger species with no or only indistinct traces of a volva; reaction with KOH often reddish brown or red. Northern Hemisphere.

*Type species: C. elegantior* (Fr. ex Fr.) Fr.

Stirps *Elegantior*. (Lamellae wax yellow or stramineous with a slight olivaceous immixture. Pileus yellowish brown or orange brown. Spores lemon-shaped.)

*C. elegantior* (Fr. ex Fr.); *C. velenovskyi* (Moser) Moser (*Phlegmacium*, Moser); *C. cereifolius* (Moser) Moser (*Phlegmacium*, Moser).

Stirps *Olivellus*. (Lamellae wax yellow to wood color. Pileus greenish to olive brownish.)

*C. olivellus* Henry.

Stirps *Fulmineus*. (Lamellae orange brown, yellow brown. Pileus orange brown, brass color, or yellowish brown, often guttate-spotted.)

*C. fulmineus* (Fr.) Fr.; *C. subfulgens* Orton; *C. alcalinophilus* Henry.

Subsect. *Coleopodes* Moser. Small species; stipe often with well-developed membranous volva; spores amygdaliform to lemon-shaped. Ammonia reaction on context not red. Under *Nothofagus* in South America.

*Type species: C. coleopus* Moser & Horak.

Stirps *Coleopus*. (Characters of the subsection.)

*C. coleopus* Moser & Horak with var. *coleopus* var. *variegatus* Moser and var. *ovatocystis* Moser; *C. vaginatus* Horak & Moser; *C. chlorophanus* Moser; *C. chrysanthus* Moser; *C. chrysophaeus* Horak.

Stirps *Pudorinus*. (Species with orange to pinkish orange pileus, lamellae and often also base; context pallid, whitish to white; spores amygdaliform to almost lemon-shaped.)

*C. aurantiovillosus* Moser; *C. pudorinus* Horak.

*Note:* The taxonomic position of this stirps is still very uncertain; with reservations we have inserted it in section *Fulvi*.

Subgenus *Sericocybe* Orton (1958). Pileus not hygrophanous, dry (only in few cases slightly viscid in wet weather and then spores subglobose), glabrous, silky, or glimmering, more rarely subtomentose. Stipe clavate-bulbous or equal. Lamellae bluish to violet. Spores amygdaliform, ellipsoid to almost globose. Context with alkalis never yellow or yellow-brown with yellow circumference around the drop. Hyphae of the cuticle never thin as in *Phlegmacium*.

*Note:* This subgenus might perhaps eventually be divided into groups that are better united with *Phlegmacium*, and others to be united with a number of non-hygrophanous species of *Telamonia*.

*Type species:* *C. alboviolaceus* (Pers. ex Fr.) Fr.

Sect. 9. *ANOMALI* Konr. & Maubl. (1948). Spores subglobose to ellipsoid or even subamygdaliform. Surface of pileus glimmery-glabrous, or squarrose, squamose-floccose (and then stipe likewise so colored).

*Type species:* *C. anomalus* (Fr. ex Fr.) Fr.

Stirps *Pholideus*. (Pileus and stipe with subsquarrose scales and floccons.)

*C. pholideus* (Fr. ex Fr.) Fr.; another species (ined.), from the Congo, seems also to belong here.

Stirps *Anomalus*. (Lamellae bluish or lilac when young. Pileus glabrous.)

*C. anomalus* (Fr. ex Fr.) Fr.; *C. caninus* (Fr.) Fr.; *C. azureus* Fr.; *C. tabularis* (Bull. ex Fr.) Fr.; *C. diabolicus* (Fr.) Fr.

Stirps *Spilomeus*. (Pileus glabrous. Lamellae bluish. Stipe with small appressed squamules which are not squarrulose.)

*C. spilomeus* (Fr. ex Fr.) Fr.

Stirps *Decoloratus*. (Lamellae argillaceous. Pileus glabrous or glimmery.)

*C. decoloratus* (Fr.) Fr.

Stirps *Nothoanomalus*. (Species with glimmery cuticle and bluish grayish to brown pileus; lamellae violet, gray to argillaceous; stipe silvery to bluish or violet; spores elliptic to amygdaliform. Under *Nothofagus* in South America.)

*C. nothoanomalus* Moser & Horak; *C. violeipes* Moser; *C. scintillatus* Moser; *C. variegatulus* Moser; *C. micaceus* Moser; *C. nitens* Moser.

Sect. 10. *SERICEOCYBE* (*Alboviolacei* Kühner & Romagnesi). Spores ellipsoid or amygdaliform. Carpophore with bluish or violet colors. Lamellae bluish or argillaceous. Odor strong, striking.

*Type species:* *C. alboviolaceus* (Pers. ex Fr.) Fr.

Stirps *Alboviolaceus*. [Pileus, lamellae, and stipe with bluish or violet colors (at least together with other pigments) and not with unpleasant odor.]

*C. alboviolaceus* (Pers. ex Fr.) Fr.; *C. kauffmanianus* Henry; *C. malachius* (Fr. ex Fr.) Fr.; *C. malachiodes* Orton; *C. pearsonii* Orton; *C. simulatus* Orton.

Stirps *Camphoratus*. (Odor disagreeable or strongly sweetish. Otherwise like preceding stirps. Lamellae bluish, vinaceous brown or ferruginous from the beginning.)

*C. camphoratus* Fr. (*C. hircinus* Fr.); *C. traganus* (Fr.) Fr.

Sect. 11. *PALLIDOVIOLACEA* Lange (1935). Carpophore whitish or argillaceous

to brown, perhaps with bluish immixtures. Spores ellipsoid or amygdaliform; rarely almost subglobose.

*Type species: C. turgidus* Fr.

Stirps *Opimus*. (Stipe robust, thick, with hard context, more or less rooting and attenuate below. Spores subglobose.)

*C. opimus* Fr.

Stirps *Turgidus*. (Stipe equal or clavate-bulbous, often very robust but not with attenuate subradicant base. Spores amygdaliform or ellipsoid.)

*C. turgidus* Fr.; *C. argentatus* (Pers. ex Fr.) Fr.; *C. hillieri* Henry; *C. suillus* Fr.; *C. rapiolens* Moser.

Subgenus **Myxacium** (Fr.) Loud. (1829 sub *Agarico*) (*Agaricus* trib. *Myxacium* Fr. 1821). Small to large fleshy species with brown, yellow, blue or vinaceous-red pigmentation, pigment epimembranal-intercellular or plasmatic. Hyphae of the cuticle 7-20 µm wide, the hyphae of the universal veil becoming gelatinized. Spores verrucose, subglobose to amygdaliform, or lemon-shaped. Cheilocystidia present or absent.

*Type species: C. collinitus* (Pers. ex Fr.) Fr.

*Note:* The gelatinizing velum universale differentiates this subgenus from all others. From *Phlegmacium* it differs moreover in the broad hyphae of the cuticle of the pileus. The limit becomes less sharp in the *Ochroleuci* and *Archeriani* in which some species have a scarcely gelatinized veil in mature carpophores, and these species have likewise the thinnest cuticular hyphae of all species of the subgenus. But they are undoubtedly closely related to other species of the same sections which are true *Myxacia* so that they were united with *Myxacium* by Lange and by the present author.

Sect. 12. *OCHROLEUCI* Konr. & Maubl. (1948). Taste more or less bitter or acrid, at least in the pellicle and mucus of the pileus. Gelatinization of universal veil not always distinct. Pigment yellow, brown, ochraceous, ivory color, and if there are blue pigments, they bleach soon and let the ochraceous component stand out. Spores small, almond- or pip-shaped.

*Type species: C. ochroleucus* (Schaeff. ex Fr.) Fr.

Stirps *Croceocaeruleus*. [Small carpophores with bluish pigments (plasmatic) in youth visible, in frondose woods.]

*C. croceocaeruleus* (Pers. ex Fr.) Fr. (*C. viola* Lange); *C. iodoides* Kauffm.

Stirps *Eburneus*. [Small to medium (30-80 mm across), with whitish pileus, in age in center often somewhat ocher, viscid to dry. In frondose, more rarely coniferous woods.]

*C. eburneus* (Velen.) Moser. (*C. emollitus* Fr. sensu Lange non Fr.; *C. cristallinus* Fr. sensu Bres. non Fr.); *C. ochroleucus* (Schaeff. ex Fr.) Fr.

Stirps *Vibratilis*. (Small to medium sized. Pileus ochraceous to orange yellow. Stipe distinctly viscid to glutinous.)

*C. vibratilis* (Fr.) Fr.; *C. pluvius* (Fr.) Fr.; *C. xantholeucus* Horak & Moser.

Stirps *Cristallinus*. (Stipe weakly viscidulous-sticky in youth, never truly glutinous. Pileus ochraceous, gilvous, fulvous, mostly also chocolate brown.)

*C. cristallinus* Fr.; *C. causticus* Fr.; *C. emollitus* Fr.; *C. pluviorum* (J. Schäffer apud Moser); *C. duramarus* (J. Schäffer apud Moser) J. Schäffer apud Moser (*Myxacium* J. Schäffer apud Moser).

Stirps *Mitis*. (Small species with ochraceous pileus, whitish to argillaceous lamellae, white to ochraceous stipe, elliptical to amygdaliform spores; taste mild. Under *Nothofagus* in South America.)

*C. mitis* Moser; *C. discoideus* Moser; *C. epileucus* Moser; *C. melleomitis* Moser & Horak.

Stirps *Paraochraceus*. (Medium sized species with yellow-brown pileus, argillaceous lamellae and more or less white, glutinous stipe; spores elliptical to amygdaliform. Under *Eucalyptus* and *Nothofagus* in Australia and South America.)

*C. paraochraceus* Moser with var. *paraochraceus* and var. *australiensis* Moser (*C. ochraceus* Clel. non Peck); *C. succineus* Moser.

Sect. 13. *PYROMYXAE* Moser & Horak. Pileus and stipe glutinous, pallid to yellowish; lamellae pallid to argillaceous; stipe cylindric to fusoid; spores elliptical to amygdaliform; hyphae of the glutinous universal veil everywhere or at least at the base of the stipe with orange red or red-brown instuction or reacting in KOH in such a manner. Under *Nothofagus* and *Eucalyptus* in South America and Australia.

Type species: *C. pyromyxa* Moser & Horak.

*C. pyromyxa* Moser & Horak; *C. erythraeus* Berk. (*C. ruber* Clel.); *C. sinapicolor* Clel.

Sect. 14. *DELIBUTI* Fr. (1836). Lamellae blue, caesious, whitish-argillaceous or yellow. Pileus and veil blue, lilac, yellow, or brownish olivaceous. Spores subglobose, ovoid, or almond-shaped. Cheilocystidia, none or basidiomorphous. Taste in all parts mild, i.e. neither bitter nor acrid. Hyphae of cuticle mostly more than 10 µm in diameter.

Type species: *C. delibutus* Fr.

Sirps *Delibutus*. (Pigment of pileus yellow, yellowish brown, olive brown, in the lamellae bluish, lilac etc. Spores subglobose.)

*C. delibutus* Fr.; *C. griseoluridus* Kauffm.

Stirps *Subglutinosus*. (Pigmentation as in the preceding stirps, but spores ellipsoid-amygdaliform.)

*C. subglutinosus* Karst.; *C. metrodii* Henry; *C. luteobrunnescens* A.H. Smith.

Stirps *Semiglobatus*. (Pilleus yellow-brown, olive-brown, or honey-brown, lamellae ochraceous to olive brown; stipe with glutinous, brown to yellow-brown veil; spores elliptical to amygdaliform. Under *Nothofagus* in South America.)

*C. semiglobatus* Moser; *C. dissimulans* Moser.

Stirps *Pallidifolius*. [Lamellae pallid (not bluish). Spores almond-shaped.]

*C. pallidifolius* A.H. Smith.

Stirps *Citrinifolius*. (Lamellae yellow. Spores almond-shaped.)

*C. citrinifolius* A.H. Smith.

Sect. 15. *MYXACIUM*. Pigment of pileus yellowish brown, red-brown, olive brownish. Lamellae blue or argillaceous brown; veil with slight bluish plasmatic pigment. Surface of stipe underneath the veil mostly more or less squamose-lacerate in adult specimens. Spores generally rather large, amygdaliform to lemon-shaped. Edge of lamellae mostly with clavate, cylindric or vesiculose sterile cells.\*

Type species: *C. collinitus* (Sow. ex Fr.) Fr.

Stirps *Fuligineoviolaceus*. (Pileus gray-brown to soot-brown; lamellae violaceous; stipe white or lilac; spores large; cheilocystidia clavate. Under *Nothofagus* in South America.)

*C. fuligineoviolaceus* Horak.

Stirps *Collinitus*. (Sterile cells, if differentiated, not vesiculose but rather basidiomorphous. Spores almond-shaped, large. Pileus brightly colored, yellow brown to red-brown. Lamellae argillaceous, brown. Stipe equal or attenuate but never striate.)

*C. collinitus* (Sow. ex Fr.) Fr.; *C. mucosus* (Bull. ex Fr.) Kickx; *C. pumilus* (Fr.) Lange; *C. alpinus* Boud.; *C. favrei* Moser ex Henderson.

Stirps *Trivialis*. (Cheilocystidia not vesiculose. Stipe equal to fusoid, usually becoming strikingly squamose-zonate, later squarrose, under the mucous layer.)

*C. trivialis* Lange (with numerous varieties) [*C. collinitus* (Sow. ex Fr.) Fr. aut plur., non Fr.; *C. mucifluus* Fr., Icon., 1884, non 1838].

Sect. 16. *DEFIBULATI* Moser. Species with large, coarsely verrucose, lemon-shaped or sublimoniform, rarely amygdaliform spores; hyphae without clamp connections in all parts of the carpophore; cheilocystidia vesiculose to clavate.

Type species: *C. elatior* Fr.

*C. elatior* Fr.; *C. pseudosalor* Lange (*C. mucifluoides* Henry; *C. integerimus* Kühn.); *C. stillatitius* Fr. (sensu Bres.); *C. mucifluus* Fr. (sensu Fr. non al.; *C. pinicola* Orton); *C. mucifluus* Fr. (sensu Ricken, Konr. & Maubl. et al., non Fr.\*\*); *C. pangloios* Moser; *C. arvinaceus* Fr.

Sect. 17. *CYSTIDIFERA* Moser. Cheilo- and pleurocystidia present, lageniform; pileus yellow-brown to brown; lamellae fuscous or violet; stipe white or violet; spores elliptical to amygdaliform. Under *Nothofagus* in South America.

\*Clamps in some North American forms absent, otherwise present. R.S.

\*\*The two different interpretations of *C. mucifluus* represent a still unsettled nomenclatorial problem.

*Type species: C. illitus* Moser & Horak.

*C. illitus* Moser & Horak; *C. absinthiacus* Moser.

Sect. 18. *MALVACEI* Moser. Smaller carpophores with whitish, lilac or pallid-flesh-colored, glutinous pileus and pallid lamellae, concolorous, clavate-bulbous stipe, amygdaliform spores. Under *Nothofagus* and (?)*Eucalyptus* in South America and Australia.

*Type species: C. malvaceus* Horak.

*C. malvaceus* Horak; *C. elaiotus* Moser; *C. austroalbidus* Clel. & Harris (*C. albidus* Clel. non Peck).

*Note:* This section is fairly isolated in subgenus *Myxacium* in spite of the glutinous stipe; a closer affinity to stirps *Lavendulensis* (*Phlegmacium*) seems possible.

Sect. 19. *ARCHERIANI* Moser. Pileus grayish blue, blue to purple; stipe with the same colors; lamellae ochre to argillaceous or concolorous with the stipe; universal veil concolorous with the surrounding surfaces of the carpophore; pileus glutinous; stipe glutinous or dry; spores globose to amygdaliform, or even lemon-shaped.

*Type species: C. archeri* Berk.

Stirps *Archeri*. (Pileus and stipe purple, violet or blue, glutinous, partial veil at least in some specimens of each population forming a membranous annulus - often in a single population or on a single mycelium specimens with cortina *and* others with a membranous annulus! -; lamellae whitish, pale argillaceous or violet; spores elliptic to amygdaliform or even lemon-shaped.

*C. archeri* Berk.; *C. magellanicus* Speg.; *C. capitellinus* Horak; *C. ajacapiae* Speg.; *C. opulentus* Moser.

Stirps *Salor*. (Pigment of veil, stipe and lamellae blue when young, or slightly lilac; spores subglobose).

*C. salor* Fr.; *C. epipoleus* Fr.; *C. betulinus* Favre.\*

Stirps *Iodes*. (Pigment in pileus, veil and lamellae blue or violet; spores ellipsoid-ovoid.)

*C. iodes* Berk. & Curt.; *C. oregonensis* A.H. Smith, *C. austrosalor* Mos., *C. subarcheri* Clel., *C. myxothecae* Horak, *C. microarcheri* Clel., *C. porphyreus* Horak, *C. caelicolor* Horak et Mos., *C. columbinus* Mos. et Hk.

Subgenus **Paramyxacium** Moser. Habit and colors similar to some species of *Myxacium* (e. gr. *C. pumilus* Lange; *C. pseudosalor* Lange; *C. elatior* Fr.) but generally only the pileus glutinous and the stipe dry; pileus membranous to somewhat fleshy, hygrophanous, at least in the marginal region, but in some species transparently striate to the center; partial veil sometimes cobweb-like but more frequently forming a membranous annulus; spores elliptic, fusoid, amygdaliform or ± lemon-shaped; hyphae with clamp connections. Under *Nothofagus* in South America.

\* Here perhaps *C. amazonicus* Sing. & Araujo, with bitter taste (as in section 12) and glutinous stipe but with subglobose spores and thin epicutis hyphae. R.S.

*Type species: C. paradoxus* Moser & Horak.

Sect. 20. *PARAMYXACIUM*. Same characters as subgenus.

*Type species: C. paradoxus* Moser & Horak.

Stirps *Paradoxus*. (Small to medium sized species; pileus transparently striate up to two thirds of the radius, glutinous, yellow-brown, fuscous, eventually with olivaceous tinge; stipe dry, often with membranous annulus, white, gray, brown or lilac; spores elliptical to amygdaliform; cheilocystidia often present.)

*C. paradoxus* Moser & Horak; *C. annulifer* Moser; *C. suppariger* Moser.

Stirps *Ochroianthinus*. (Pileus medium-sized, slightly fleshy, ochraceous yellow to yellow-brown, on the margin transparently striate; lamellae ocher to brown; stipe violet, dry or glutinous, with membranous or glutinous annulus; spores amygdaliform.)

*C. ochroianthinus* Horak & Moser; *C. gliocyclus* Horak.

Stirps *Myxacioides*. (Small carpophores with the pileus transparently striate over two thirds of the radius, yellow-brown; stipe violet; cortina present; spores fusoid.)

*C. myxacioides* Moser; *C. semiamictus* Horak.

Stirps *Brunneoolivascens*. (Pileus yellow-brown to olive-brown, olive-gray, transparently striate over two-thirds of the radius; stipe dry, white, gray or brownish, partial veil cortinoid; spores elliptic to amygdaliform.)

*C. brunneoolivascens* Moser; *C. pellucidus* Moser.

Subgenus *Telamonia* (Fr. 1821) Loudon 1829 (as subgenus of *Agaricus*).

Carpophores small and membranous to large, robust and fleshy; pileus mostly hygrophanous and non-viscid, exceptionally glutinous; with double veil but only the cortina always distinctly developed, universal veil in youth also always present but frequently soon becoming indistinguishable while, in other species, it is often or constantly very strongly developed and forms belt-like annular or floccose zones on the stipe and may be visible also on the surface of the pileus; cuticle of the pileus consisting of thin or thick (4-20 µm) hyphae; trama of the pileus regular (subparallel radial hyphae), interwoven or subcellular-shortened; spores amygdaliform, ovoid, ellipsoid or subglobose, ornamented (from verrucose to subsMOOTH), yellow-brown under the microscope, without germ pore and without a very strong callus, without suprahilar plage; pigments predominantly incrusting and intercellular, and brown, insoluble in the usual organic solvents (alcohol, ether, chloroform, acetone, ethyl-acetate, etc.), but violet tinged plasmatic pigments frequently also present although rarely predominant; sometimes yellow or red (vacuolar?) pigments present in the veil. On earth, almost exclusively in forests and in the Salicetum and Betuletum of the alpine and arctic zone, mostly ectomycorrhizal with forest trees and shrubs, but some also endomycorrhizal with Ericaceae (Vaccinoideae).

*Type species: C. decipiens* (Pers. ex Fr.) Fr.

Sect. 21. *MYXOTELAMONIA* Moser. Characters of the subgenus; colors gray to

brown both on pileus and lamellae; stipe whitish to brown; epicutis strongly gelatinized and surface of pileus glutinous. Under *Nothofagus* in South America, also (under *Eucalyptus*?) in Australia.

*Type species: C. cinereobrunneus* Moser.

*C. cinereobrunneus* Moser; *C. ombrophilus* Moser; *C. hydrocephalus* Moser; *C. phaeocephalus* Horak; *C. castaneofulvus* Clel.

Sect. 22. *TENUIORES* Fr. Small species with membranous pileus which is more or less acute to flat-conic or with papilla, transparently striate when moist; universal veil either white or very slightly ocher tinged, or so weakly developed that it is scarcely visible on the adult carpophore; spores ellipsoid-amygdaliform.

*Type species: L. leucopus* Fr.

Stirps *Acutus*. (Universal veil of adult carpophore not distinguishable, weak in young specimens; edge of lamellae with cheilocystidia.)

*C. acutus* (Pers. ex Fr.) Fr.; *C. junghuhnii* Fr.; *C. boyacensis* Sing.

Stirps *Austroacutus*. (Species similar to those of the preceding stirps, but color darker reddish brown in humid condition; cheilocystidia absent. Under *Nothofagus* in South America.)

*C. austroacutus* Moser; *C. subconicus* Moser; *C. squamiger* Moser; *C. cucullatus* Moser; *C. citrinopigmentatus* Moser.

Stirps *Incisus*. (Veil more strongly developed than in preceding stirps, white. Pileus  $\pm$  acutely conical, brown. Cheilocystidia none.)

*C. incisus* (Pers. ex Fr.) Fr.; *C. parvannulatus* Kühner; *C. parvulus* Henry; *C. striaepileus* Favre; *C. striatulus* Cleland.

Stirps *Fasciatus*. (Pileus campanulate-conical, membranous, striate. Odor not significant. Stipe with white to ocher-rusty velar fibrils.)

*C. fasciatus* (Scop. ex Fr.) Fr.; *C. pulcher* Peck (*C. nanus* Killermann); *C. luci* Henry.

Stirps *Cedriolens*. (Somewhat larger species with a stipe up to 100 mm long. Pileus more applanate-conical with acute papilla. Odor aromatic.)

*C. cedriolens* Moser.

Stirps *Phenolicus*. (Small brown species with a pileus rarely over 10 mm broad and the stipe likewise brownish or brown; veil white or fugacious; odor of phenol. Under *Nothofagus* in South America.)

*C. phenolicus* Moser (a second species is insufficiently known).

Stirps *Leucopus*. (Small species with brown pileus and lamellae and white to whitish stipe, without recognizable veil; spores elliptical-amygdaliform.)

*C. leucopus* Fr.; *C. riopancensis* Moser.

Stirps *Avellaneus*. (Smaller species with long stipe and conic to campanulate

pileus, hazel to reddish brown; stipe white or whitish, without recognizable veil; spores generally  $> 10 \mu\text{m}$  long. Under *Nothofagus* in South America.)

*C. avellaneus* Moser; *C. flaoconicus* Moser; *C. jaganicus* (Speg.) Horak (Tricholoma, Speg.).

Stirps *Erebius*. (Carpophores small to medium-sized with brown pileus and slender stipe which is whitish, gray or pallid, without a distinct veil; spores scarcely more than  $10 \mu\text{m}$  long. Under *Nothofagus* in South America.)

*C. erebius* Moser; *C. tephrophyllus* Moser; *C. scolecinus* Moser; *C. geosmus* Moser.

Stirps *Tenellus*. (Carpophores small; pileus brown, rufous, lamellae ocher to argillaceous; stipe dirty whitish to brown, with or without whitish or yellowish veil; spores elliptical, less than  $10.5 \mu\text{m}$  long. Under *Nothofagus* in South America.)

*C. tenellus* Moser; *C. catervatus* Moser; *C. perlaetus* Horak; *C. sericeoochraceus* Moser; *C. macilentus* Moser; *C. aridus* Moser; *C. tenuis* Moser; *C. pachynemeus* Moser; *C. elachus* Moser.

Stirps *Luteifolius*. (Small carpophores; lamellae yellow, ocher-yellow or bright yellow-brown; stipe often with yellow tinge; veil yellow or ocher; spores amygdaliform, up to  $12.5 \mu\text{m}$  long. Under *Nothofagus* in South America.)

*C. luteifolius* Moser & Horak; *C. brevisporus* Moser; *C. vinaceomaculatus* Moser; *C. viridibasalis* Moser; *C. luteolus* Moser; *C. xanthopus* Moser; *C. mendicus* Moser.

Stirps *Paludicola*. (Small carpophores growing in humid habitats, with pale brownish and olivaceous colors both on pileus and lamellae and also on the stipe; spores elliptical-amygdaliform, up to  $12.5 \mu\text{m}$  long; under *Nothofagus* in South America).

*C. paludicola* Moser; *C. brunneovirescens* Moser.

Stirps *Scabrosporus*. (Small brown carpophores with coarsely verrucose, broadly elliptical to subglobose spores. Under *Nothofagus* in South America.)

*C. scabrosporus* Moser; *C. margaritisporus* Moser; *C. humilis* Moser.

Stirps *Focalis*. (Small carpophores with dark fuscous to umber colors; stipe whitish, with membranous ring-belt; spores elliptical to amygdaliform; under *Quercus* in Colombia.)

*C. focalis* Moser.

Stirps *Obtusus*. (Smaller species, with the stipe often rather long, subradicant.)

*C. obtusus* (Fr.) Fr.; *C. scandens* Fr.; *C. fulvescens* Fr.

Stirps *Candelaris*. (Medium-sized species. Stipe unicolorous; orange brown not with longitudinal fibrillose stripes.)

*C. candelaris* Fr.

**Stirps Angulosus.** [Pileus yellow brown to orange brown (with an apricot tinge). Stipe characteristically longitudinally fibrillose.]

*C. angulosus* Fr., *C. renidens* Fr.

Sect. 23. *ILIOPODII* Fr. (1838) (*Leptophylli* Fr. 1874; *Platyphylli* Fr. 1874). Rather small species, pileus not fleshy, convex or obtusely conical with dark brown epimembranous-intercellular pigment (also in stipe). Veil usually well developed, white, forming one or several belt-like zones. Hyphae of cuticle of pileus not broader than 10  $\mu\text{m}$ .

*Type species:* *C. iliopodius* (Bull. ex Fr.) Fr. sensu Moser and Bull. and Fr.

**Stirps Rigidus.** (Pileus mostly more or less obtuse. Odor not aromatic. Spores ovoid-amygdaliform, not reaching twice as long as broad.)

*C. rigidus* (Scop. ex Fr. apud Weinm.) Fr.; *C. iliopodius* (Bull. ex Fr.) Fr. sensu Moser and Bull. and Fr.

**Stirps Heterosporus.** (Spores at least twice as long as broad).

*C. heterosporus* Bres.; *C. adalberti* Favre; *C. fibrillosus* Cleland; *C. fusisporus* Kühner.

**Stirps Paleaceus.** (Aromatic odor frequently present. Color with grayish or lilac immixture. Veil white. Pileus often finely squamulose, obtuse to acutely conical; spores elliptical to subglobose. In coniferous and frondose woods.)

*C. paleaceus* Fr.; *C. flexipes* (Pers. ex Fr.) Fr.; *C. hemitrichus* (Pers. ex Fr.) Fr.; *C. microcyclus* Fr.; *C. muscicola* A.H. Smith; *C. comptulus* Moser.

**Stirps Alnetorum.** (Pileus acutely conical. Veil white, abundant to sparse, often somewhat blackening. Associated with frondose trees, particularly *Alnus*.)

*C. alnetorum* (Velen.) Moser; *C. fagetorum* Moser; *C. nigricans* (Velen.) Sing. (p.p.?) ; *C. atropusillus* Favre; *C. tucumanensis* Moser; *C. parabibulus* Moser.

**Stirps Egenus.** (Small brown species with white to pale brownish veil on stipe and sometimes also on pileus; spores ellipsoid to amygdaliform. Under *Nothofagus* in South America.)

*C. egenus* Horak; *C. hebes* Horak; *C. laetifolius* Horak; *C. maulensis* Moser; *C. squamiger* Moser.

**Stirps Lignyotus.** (Small, dark-brown species - dark on pileus, lamellae and stipe; spores elliptical-amygdaliform. Under *Nothofagus* in South America.)

*C. lignyotus* Horak; *C. fuscus* Moser; *C. umbrinus* Moser.

Sect. 24. *HYDROCYBE* Chev. (ut sect. *Agarici*, 1826). Rather small species with pinkish lilac or violet colors in the stipe, eventually also in the lamellae or in the entire carpophore.

*Type species:* *C. decipiens* (Pers. ex Fr.) Fr.

**Stirps Decipiens.** (Stipe pink, flesh brownish. Spores smaller than 9  $\mu\text{m}$ . Veil white.)

*C. decipiens* (Pers. ex Fr.) Fr.; *C. atrocaeruleus* Moser.

Stirps *Erythrinus*. (Stipe pinkish lilac. Spores often more than 9  $\mu\text{m}$  long. Veil whitish or grayish brown, weak, or none.)

*C. erythrinus* (Fr. ex Secr.) Fr.; *C. sertipes* Kühner; *C. subserotypes* Romagnesi (*C. unimodus* Britz.?); *C. washingtonensis* A.H. Smith.

Stirps *Ionipus*. (Small carpophores with brown pileus, lilac lamellae and lilac stipe (at least at the apex); spores elliptical to amygdaliform. Under *Nothofagus*\* in South America.)

*C. ionipus* Horak; *C. atroacutus* Horak & Moser; *C. exilis* Horak.

Stirps *Pulchripes*. (Species with more pronounced development of bluish violet pigments in both stipe and lamellae.)

*C. pulchripes* Favre; *C. multicolor* Moser; *C. paranomalus* Henry.

Stirps *Bibulus*. [Entire carpophore violet. Veil white if present, but varying from strongly to very weakly (and scarcely visible) developed.]

*C. bibulus* Quél. (*C. pulchellus* Lange; *C. americanus* A.H. Smith; *C. insignis* Britz.).

Stirps *Obscurus*. (Small to medium-sized carpophores with gray, violet, or violet-brownish or dark blue colors on the pileus and stipe and also often on the lamellae; spores elliptical. Under *Nothofagus* in South America.)

*C. obscurus* Moser; *C. lugubris* Moser; *C. violaceoolivascens* Moser; *C. parazureus* Horak; *C. lividus* Moser; *C. lazulinus* Horak & Moser; *C. janthinophaeus* Horak & Moser.

Sect. 25. *HELVELLOIDEI* Moser. Smaller species; stipe covered by a yellow to brown veil, sometimes pileus also more or less fibrillose from the veil; hyphae of veil broad (7-20  $\mu\text{m}$ ) and wall incrusted.

Type species: *C. helvelloides* (Fr.) Fr.

Stirps *Helvelloides*. (Growing with *Alnus*; veil yellow, yellow-brown, pale brown; lamellae thick, distant, grayish violet, gray-brown, dark brown.)

*C. helvelloides* (Fr.) Fr.; *C. pachythrix* Moser; *C. alneus* Moser; *C. badiovestitus* Moser.

Stirps *Arenatus*. (Growing in coniferous woods, brown in all parts; veil yellow brown to brown; pileus often squarrose-scaly; lamellae not thick and distant.)

*C. arenatus* Fr.; *C. psammocephalus* Fr.; *C. strobilaceus* Moser; *C. angelesianus* A.H. Smith.

\**C. galeriniformis* Sing. & Araujo may belong here; it is neotropical and independent of *Nothofagus*. — Two other species from the Amazonas region, *C. umbilicatus* Sing. & Araujo and *C. campinaranae* Sing. & Araujo likewise belong in subgenus *Telamonia* but cannot be placed further. R.S.

*Stirps Semivestitus*. (Small brown carpophores with strongly developed peronate veil which is ochraceous to brown; generally associated with *Salix*).

*C. semivestitus* Moser; *C. gausapatus* Favre; *C. cucumisporus* Moser; *C. rusticellus* Favre; *C. pertristis* Favre.

*Stirps Polyadelphus*. (Very small brown carpophores with ochraceous veil consisting of very broad hyphae; numerous carpophores on a common mycelial subiculum; spores small, subglobose to broadly elliptical. On dead leaves of *Nothofagus* in South America.)

*C. polyadelphus* Moser.

Sect. 26. *FIRMIORES* Fr. (1838). Species with white or violet stipe; veil white, very weakly to strongly developed. Pileus brown or with violet pigment.

Type species: *C. armeniacus* (Pers. ex Fr.) Fr.

Subsect. *Armeniaci* Moser. Stipe thin, white, or sometimes slightly lilac at apex, sometimes more or less radicant. Veil hardly distinguishable or weakly developed.

Type species: *C. armeniacus* (Pers. ex Fr.) Fr.

*Stirps Armeniacus*. (Color of pileus rather brightly yellow brown, orange yellow; stipe white-silky without visible rests of the universal veil.)

*C. armeniacus* (Pers. ex Fr.) Fr.; *C. dilutus* (Pers. ex Fr.) Fr.; *C. cinnamomeobadius* Cleland; *C. picosporus* Moser.

*Stirps Hoeftii*. (Colors pale ochraceous to bright ochraceous, at times with olive tone. Lamellae ochraceous.)

*C. hoeftii* (Weinm.) Fr.; *C. abiegnus* Britz.

*Stirps Rigens*. [Pileus smaller than in previous stirps (viz. here 20-30 mm in diameter). Stipe without visible universal veil, radicant without thickening.]

*C. rigens* (Pers. ex Fr.) Fr.

*Stirps Albocinctus*. (Pileus yellow to fulvous; lamellae clay color to ferruginous; stipe white, cylindric to clavate; spores elliptical-amygdaform and up to 12  $\mu$ m long; veil white, strongly developed, both on the stipe and on the margin of the pileus. Under *Nothofagus* in South America.)

*C. albocinctus* Moser; *C. obscuroarmeniacus* Moser; *C. mesophaeus* Moser; *C. chusqueae* Moser; *C. leucoloma* Moser; *C. elaphinus* Moser; *C. nothodamascenus* Moser; *C. ochraceolamellatus* Moser; *C. naucinus* Moser; *C. nitellinus* Moser.

*Stirps Latifolius*. (Pileus reddish brown, umber brown, or blackish brown, with very broad, dark brown lamellae; stipe white to brownish in age; spores broadly elliptical to subglobose.)

*C. latifolius* Moser.

*Stirps Singeri*. (Pileus dark red-brown to umber brown; stipe whitish to brownish in old specimens; spores elliptical to amygdaliform.)

*C. singeri* Moser; *C. purpureobrunneus* Moser; *C. dichrous* Moser; *C. turpis* Horak.

Stirps *Duracinus*. [Stipe white (at times at apex lilac), mostly more or less fusoid-radicant. Universal veil weakly distinguishable. Odor none, or raphanaceous; pileus exceptionally glutinous.]

*C. duracinus* Fr. with var. *duracinus* var. *raphanicus* Moser; *C. pseudoduracinus* Henry; *C. pseudocandalaris* (Moser) Moser (Hygrocybe, Moser; *C. candalaris* ss. Ricken); *C. phaeophyllus* Karst.; *C. vilior* Karst; *C. austroduracinus* Moser; *C. cylindrospermus* Moser; *C. contractus* Henry; *C. myxoduracinus* Horak.

Subsect. *Bicolorini* Moser. Stipe always, at least in part, with violet plasmatic pigment. Colors of pileus dark brown, violet brown, also violet-lilac. Rhapanaceous odor mostly distinct.

Type species: *C. bicolor* Fr.

Stirps *Bicolor*. (Stipe bicolorous, violet above, white below. Odor distinctly rhapanaceous.)

*C. bicolor* Lange; *C. castaneus* (Bull. ex Fr.) Fr.; *C. saturninus* (Fr.) Fr.

Stirps *Evernius*. (Pileus brown; lamellae ferruginous-brown. Stipe violet or lilac, at times with a white velar zone, often attenuate towards the base. Odor raphanaceous or not.)

*C. evernius* (Fr. ex Fr.) Fr.; *C. cinnamoviolaceus* Moser; *C. parevernius* Henry.

Stirps *Scutulatus*. (Stipe and lamellae, and sometimes also pileus violet or lilac. Stipe with one or several white velar zones. Base mostly attenuate, with or without raphanaceous odor.)

*C. scutulatus* (Fr.) Fr.

Stirps *Deceptivus*. (Carpophores medium-sized with violet colors on young pileus and stipe - eventually also lamellae and veil -; stipe cylindric or with attenuate base; spores elliptical; odor not raphanaceous. Northern and Southern Hemisphere.)

*C. deceptivus* Kauffm.; *C. pumanquensis* Moser.

Subsect. *Bivelini* Moser. Stipe white with distinct velar zones; carpophores slender to robust and with broad stipe.

Type species: *C. bivelus* (Fr. ex Fr.) Fr.

Stirps *Bivelus*. (Pileus ochraceous brown to reddish brown. Lamellae ochraceous to yellowish ferruginous or brown. Stipe white, at least in youth, and covered by a white veil which forms one or several belts, stipe cothurnate-sheathed with it.)

*C. bivelus* (Fr. ex Fr.) Fr.; *C. triformis* Fr.; *C. biformis* Fr.; *C. melleopallens* Fr.; *C. licinipes* Fr.; *C. bulbosus* (Sow. ex Fr.) Fr.; *C. phellochrous* Horak.

Stirps *Laniger*. (Pileus and lamellae a very deep and bright ferruginous orange, ferruginous brown. Veil strongly developed.)

*C. laniger* Fr.

Subsect. *Lilacifolii* Moser. Pileus hygrophanous, ± fleshy; lamellae and at least the apex of the stipe with lilac, violet or vinaceous tints; conspicuous veil absent. Under *Nothofagus* in South America.

Type species: *C. roseopurpurascens* Moser & Horak.

Stirps *Roseopurpurascens*. (With lilac or violet colors and broadly elliptical, extremely strongly verrucose spores.)

*C. roseopurpurascens* Moser & Horak; *C. pachythelis* Moser.

Stirps *Xerampelinus*. (With vinaceous red to brown colors; spores elliptical to agygaliform.)

*C. xerampelinus* Horak.

Sect. 27. *TELAMONIA*. Medium-sized to large fleshy species with the stipe distinctly more or less brownish colored, also pileus brownish; at times with lilac or violet colors intermixed. Universal veil weakly to strongly developed.

Type species: *C. torvus* (Fr. ex Fr.) Fr.

Subsect. *Torvini* Moser. In the stipe, the brown pigments are more or less intermixed with violet ones, at times also in pileus and lamellae with violet tones.

Type species: *C. torvus* (Fr. ex Fr.) Fr.

Stirps *Torvus*. (Young pileus violet, lilac or whitish in part or entirely. Robust species with broad stipe sometimes with strongly developed universal veil.)

*C. torvus* (Fr. ex Fr.) Fr.; *C. umidicola* Kauffm.; *C. subviolascens* Henry.

Stirps *Cypriacus*. [Violet colors in pileus (aside from brown ones) present, but carpophores smaller with more slender stipe.]

*C. cypriacus* Fr.; *C. livor* Fr.; *C. sciophyllus* Fr.

Stirps *Cinereus*. (Pileus, lamellae and stipe gray, bluish gray; spores elliptical. Under *Nothofagus* in South America.)

*C. cinereus* Moser.

Stirps *Lucorum*. (Robust fleshy species, but violet or lilac colors only in the stipe.)

*L. lucorum* (Fr.) Lange; *C. impennis* Fr.; *C. divulgatus* Britz.

Subsect. *Privigni* Moser. Brown-stemmed species with poorly developed universal veil. Colors varying from ochraceous to red-brown, also cervinous or umber.

Type species: *C. privignus* (Fr. ex Weinm.) Fr.

Stirps *Privignus*. (Stipe more or less clavate or even bulbous and pileus, because of sparse velar remainders, appearing characteristically glimmery-silky dry.)

*C. privignus* (Fr. ex Weinm.) Fr.; *C. privignoides* Henry; *C. privignorum* Henry.

Stirps *Subferrugineus*. (Stipe with clavate-thickened base, often fasciculate, in all parts rather dull brown; surface of pileus not glimmery-silky.)

*C. subferrugineus* (Batsch ex Fr.); *C. imbutus* Fr.; *C. subbalaustinus* Fr.; *C. holophaeus* Lange ex Lange.

Stirps *Macropus*. (Stipe 2-4 times as long as diameter of pileus. Large fleshy species. Not so deeply brown, base white.)

*C. macropus* (Fr.) Fr.

Stirps *Balaustinus*. (Color ochraceous brown to fulvous, or violet brownish, cervinous, etc. Spores subglobose.)

*C. balaustinus* Fr.; *C. multivagus* Britz.

Stirps *Carneolus*. (Fleshy carpophores with red-brown pileus, white to flesh-brown stipe and white to pale brownish veil; pileus not hygrophanous; spores elliptical to amygdaliform. Under *Nothofagus* in South America.)

*C. carneolus* Moser & Horak; *C. carneoalbus* Moser; *C. carneocrassus* Moser.

Stirps *Perochraceus*. (With characteristic pale ocher brown to yellow-brown colors in all parts, pileus very slightly hygrophanous; spores elliptical to amygdaliform. Under *Nothofagus* in South America.)

*C. perochraceus* Moser.

*Note:* The position of this stirps is still uncertain.

Stirps *Concolor*. (Pileus and stipe yellow-brown, yellow-ferruginous; lamellae pale ocher brown; spores elliptical to amygdaliform. Under *Nothofagus* in South America.)

*C. concolor* Horak; *C. flavoferrugineus* Moser.

*Note:* The position of this stirps is still uncertain.

Subsect. *Hinnuloidei* Moser (ined.). Lamellae distant, adnexed-seceding. Carpophores ochraceous to cervinous. Stipe slender, with or without a velar zone.

*Type species:* *C. hinnuleus* Fr.

*C. hinnuleus* Fr.

Subsect. *Brunnei* Moser. Carpophores with very dark umber brown colors, eventually blackish brown or even blackening, small, medium, or large. White velar zone present, or else blackening when old.

*Type species:* *C. brunneus* (Pers. ex Fr.) Fr.

Stirps *Uraceus*. (Carpophore medium sized to large, in age entirely or partly blackening.)

*C. uraceus* Fr.; *C. rubricosus* Fr. ex Fr.; *C. crassifolius* (Velen.) Moser.

Stirps *Macilenthosporus*. (Pileus brown; lamellae and stipe likewise brown; spores narrow, elliptical to fusiform. Until now known only from Jamaica, W.I., with *Pinus*.)

*C. macilenthosporus* Moser.

*Stirps Brunneus*. (Medium sized to fleshy species of dark umber color on pileus, lamellae and stipe, the latter showing a distinct velar zone which is white.)

*C. brunneus* (Pers. ex Fr.) Fr.; *C. glandicolor* (Fr.) Fr.; *C. stemmatus* Fr.; *C. punctatus* (Pers. ex Fr.) Fr.; *C. pachypus* Moser.

Sect. 28. *BOVINI* Moser. Rather fleshy species, remarkable because of their fuscous or brown universal veil.

Type species: *C. bovinus* Fr.

*Stirps Bovinus*. (Carpophore brown in all parts without olive or lilac secondary pigments; Northern and Southern Hemisphere.)

*C. bovinus* Fr.

*Stirps Brunneovelatus*. (Larger carpophores with umber to red-brown colors in all parts, pale to bright -, with clavate to bulbous stipe, with fuscous belts from the universal veil; spores elliptical to amygdaliform, up to 12  $\mu\text{m}$  long. Under *Nothofagus* in South America; under *Eucalyptus* in Australia.)

*C. brunneovelatus* Moser & Horak (with var. *rugosus* Moser); *C. siccus* Moser; *C. rufobrunneus* Moser; *C. limbatus* Moser; *C. veronabrunneus* Cleland.

*Stirps Lasiospermus*. (Smaller to medium sized carpophores with pileus, lamellae and stipe sometimes with grayish violet tinge; spores broadly elliptical to subglobose, coarsely verrucose. Under *Nothofagus* and *Eucalyptus*, South America, Jamaica, Australia.)

*C. lasiospermus* Moser; *C. trachyspermus* Moser; *C. vinaceocinereus* Clel.

*Stirps Fuscooperonatus*. (Stipe in upper portion with lilac tinge; pileus scaly punctate from veil.)

*C. fuscooperonatus* Kühn. (*Hydrocybe tigrina* Moser non *Cortinarius tigrinus* Johns.); *C. canabarba* Moser.

Sect. 29. *ARMILLATI* Moser. Species characterized by a red or deep red-brown universal veil.\*

Type species: *C. armillatus* (Fr. ex Fr.) Fr.

Subsect. *Armillati* Moser. Veil well-developed in form of belt-like zones.

Type species: *C. armillatus* (Fr. ex Fr.) Fr.

*Stirps Armillatus*. (Veil cinnabarinous.)

*C. armillatus* (Fr. ex Fr.) Fr. with var. *luteoornatus* Moser; *C. haematochelis* (Bull. ex) Fr.

\*In the light of pigment analysis, a rearrangement of subsections and stirpes in this section may become necessary since *C. armillatus* and probably also *C. rubrobasalis* Moser & Horak contain dermolutein and dermorubin in the veil (pigments known from *Dermocybe sanguinea*) whereas *C. bulliardii* and *C. pseudocolos* contain cinnarubin and cinnalutein (pigments known from *Dermocybe cinnabarina*). Hitherto only these four species have been examined. For this reason we prefer to conserve for the time being the taxonomy used in the earlier editions.

Stirps *Paragaudis*. (Veil red-brown to vinaceous brown; other colors not as in the following stirps.)

*C. paragaudis* Fr.; *C. veregregius* Henry; *C. subtestaceus* A.H. Smith, possibly *C. badiovinaceus* Moser.

Stirps *Boulderiensis*. (Veil vinaceous brown. Lamellae gray-lilac, vinaceous gray; apex of stipe violet.)

*C. bulderiensis* A.H. Smith with var. *pallidulus* Favre.

Subsect. *Miniatopodes* Moser. Veil not forming belt-like zones but covering the lower portion of the stipe, sometimes also the margin of the pileus.

Type species: *C. miniatopus* Lange.

Stirps *Miniatopus*. (Pileus, stipe, and lamellae with more or less ochraceous to ochraceous brown colors. Small, almost membranous species.)

*C. miniatopus* Lange with var. *konradi* Moser var. *subalpinus* Moser; *C. praestigiosus* (Fr.) Moser.

Stirps *Colus*. (Colors more red-brown, fulvous. Medium sized, rather fleshy species. Lamellae brown.)

*C. colus* Fr.; *C. pseudocolus* Moser; *C. rubrobasalis* Moser & Horak; *C. basirubescens* Clel. & Harris.

Stirps *Bulliardii*. (Lamellae and/or apex of stipe violet tinged in youth.)

*C. bulliardii* (Pers. ex Fr.) Fr.; *C. rubripes* Kauffm.; *C. erythroionipus* Fayod possibly also *C. danili* Henry; *C. aurantiomarginatus* J. Schäffer.

Sect. 29. *VIRIDICANTES* Moser. Pileus and stipe olivaceous; lamellae olivaceous to lilac; pileus viscid or not. Under *Nothofagus* in South America.

Type species: *C. olivellostriatus* Moser.

Stirps *Olivellostriatus*. (Pileus membranous to slightly fleshy; pileus, lamellae, and stipe olivaceous brown; pileus glutinous; spores elliptical-amydaliform, verrucose; cheilocystidia present, balloon-shaped.)

*C. olivellostriatus* Moser.

Stirps *Tristis*. (Pileus and stipe olive to olive brown; lamellae lilac; carpophores medium sized, slender; spores amygdaliform.)

*C. tristis* Horak.

Subgenus *Leprocybe* Moser. Strongly yellow, green or blue fluorescent substances present, especially in the lamellae but also in the hyphae of the trama; hyphae of the (cutis-like) epicutis rather broad, often incrusted; surface of pileus fibrillose to squamulose, rarely silky, colored olive, yellow, yellow-brown, brown, rarely reddish; spores subglobose to broadly elliptical, rarely elliptical.

Type species: *Cortinarius cotoneus* Fr.

Sect. 31. *LEPROCYBE*. Carpophores with olive, rarely only yellow to yellow-brown colors; universal veil ocher, yellow, greenish yellow, olive brown, brown, sepia to blackish brown or reddish; odor often raphanaceous; taste unpleasant; spores subglobose to short elliptical; a bright yellow to yellow-green fluorescence noticeable under ultraviolet light.

*Type species: C. cotoneus* Fr.

Stirps *Ignipes*. (With red universal veil; spores short-elliptical.)

*C. ignipes* Moser.

Stirps *Cotoneus*. (Larger species with olive green to olive yellow colors in all parts; universal veil olive brown to sepia or nearly blackish brown, ± peronate.)

*C. cotoneus* Fr.; *C. phrygianus* (Fr.) Fr.; *C. melanotus* Kalchbr.; also some interesting species from Borneo, still unpublished.

Stirps *Psittacinus*. (Similar to preceding stirps but veil yellow or yellow-green.)

*C. psittacinus* Moser; *C. mellinus* Britz.; *C. croceocolor* Kauffm.; *C. annulatus* Peck; *C. flavifolius* Peck; possibly also *C. subnotatus* Fr.

Stirps *Raphanoides*. (Smaller species with more or less olive to green colors and yellow to greenish veil; spores globose.)

*C. raphanoides* (Pers. ex Fr.) Fr.; *C. subannulatus* J. Schäffer & Moser; *C. venetus* (F. ex Fr.) Fr. with var. *montanus* Moser; *C. clandestinus* Kauffm.; *C. chrysolithus* Kauffm.

Stirps *Zinziberatus*. (Pileus silky, smooth, brown with olivaceous tinge; veil yellow to greenish; spores short-elliptical.)

*C. zinziberatus* (Scop. ex Fr.) Fr.; *C. isabellinus* (Batch. ex Fr.) Fr.

Sect. 32. *BRUNNEOTINCTI*. Moser. Carpophore in all parts with brown colors, but always with olivaceous hue; epicutis with loosely interwoven broad hyphae; spores globose; a blue-green fluorescent substance present.

*Type species: Cortinarius betuletorum* Moser. - Only the type species is known to belong here with certainty.

Sect. 33. *LIMONII* Moser. Pigment orange brown to yellow; universal veil yellow; one or more yellow fluorescent substances present; spores subglobose to globose or broadly elliptical; epicuticular hyphae somewhat narrower than in the preceding sections.

*Type species: C. limonius* (Fr. ex Fr.) Fr.

Stirps *Limonius*. (Medium sized carpophores with lemon yellow veil; pileus-surface smooth to furfuraceous or very slightly scaly.)

*C. limonius* (Fr. ex Fr.) Fr.; *C. distans* Peck (with var. *olympianus* A.H. Smith).

Stirps *Gentilis*. (Smaller species with yellow universal veil.)

*C. gentilis* (Fr.) Fr.; *C. saniosus* (Fr.) Fr.; *C. nothosaniosus* Moser.

Stirps *Callisteus*. (Veil poorly developed and not recognizable in mature specimens; stipe clavate, sometimes even bulbous; pileus smooth to scaly.)

*C. callisteus* (Fr. ex Fr.) Fr.; possibly also *C. tofaceus* Fr. and its var. *redimitus* Fr.

*Note:* The position of this stirps is not quite certain.

Stirps *Humicola*. (Pileus and stipe - up to the cortina - very distinctly scaly; context pallid.)

*C. humicola* (Quél.) Maire.

*Note:* The position of this stirps is not quite certain.

Sect. 34. *ORELLANI* Moser. Pileus and lamellae with orange-brown to cinnamon colors, stipe also sometimes so colored; universal veil yellow but not always recognizable; spores subglobose to broadly elliptical or elliptical; with bright blue or blue-green-fluorescent substances.

*Type species:* *C. orellanus* Fr.

Stirps *Orellanus*. (Fluorescence blue; lamellae and pileus more or less orange brown. Toxic.)

*C. orellanus* Fr.; *C. speciosissimus* Kühn. & Romagnesi.

Stirps *Fluorescens*. (Stipe and veil bright yellow, lemon yellow; fluorescence extremely bright, bluish green. Under *Nothofagus* in South America.)

*C. fluorescens* Horak.

Sect. 35. *BOLARES* K. & R. ex Moser. With orange brown to reddish brown colors or with red scales on pileus and stipe; context ± yellow when bruised, spores subglobose to elliptical. The blue fluorescence is similar to that of the preceding section.

*Type species:* *C. bolaris* (Pers. ex Fr.) Fr.

Stirps *Bolaris*. (Pileus and stipe with red to ferruginous scales; spores subglobose to broadly elliptical.)

*C. bolaris* (Pers. ex Fr.) Fr.; possibly also *C. pavonius* Fr.

Stirps *Rubicundulus*. (Pileus reddish brown; stipe pale ochraceous; spores narrowly elliptical.)

*C. rubicundulus* (Rea) Pearson.

Subgenus *Cystogenes* Moser. Rather small to rather large fleshy species with orange to rufous or brown pileus, yellow or olive greenish, more rarely brown to whitish brown stipe, ocher or yellow or green, ferruginous to fuscous universal veil; spores subglobose to amygdaliform; pleuro- and cheilocystidia mostly differentiated; no fluorescent substances under ultraviolet light.

*Type species:* *C. formosus* Moser.

Sect. *CYSTOGENES*. Characters of the subgenus.

*Type species:* *C. formosus* Moser.

Stirps *Austrolimoneus*. (Medium sized carpophores; pileus not hygrophanous, bright orange brown to red-brown; stipe yellow or exceptionally flesh-white; veil ocher-orange-brown to red-brown or fuscous; spores subglobose to elliptical.)

*C. austrolimoneus* Moser & Horak with var. *austrolimoneus* and var. *ochrovelatus* Moser; *C. xylocinnamomeus* Moser; with var. *xylocinnamomeus* and var. *fuscoornatus* Moser; *C. semirubricundulus* Moser; *C. limonioides* Moser; *C. cinnamophyllus* Moser; *C. teraturgus* Moser.

Stirps *Formosus*. (Small to very large carpophores with red-brown to dark brown pileus, with olivaceous to yellowish ferruginous lamellae and yellowish- to olive-greenish stipe; spores elliptical to amygdaliform; typical cystidia often present, these brown-granulose-incrusted, at least in some state of development.)

*C. formosus* Moser; *C. diemii* Moser; *C. trachycystis* Moser; *C. leptocystis* Moser; *C. rigidipes* Moser (*C. uraceus*, Fr. sensu Kühner).

Stirps *Strictipes*. (Similar to stirps *Formosus*, with brown and olive greenish colors, but without any cystidia.)

*C. strictipes* Moser.

*Note:* The position of this stirps is at present uncertain.

Stirps *Excruciatus*. (Pileus chestnut brown; lamellae ocher brown; stipe brown with white base; spores elliptical; cheilo- and pleurocystidia very characteristically fusoid to lageniform.)

*C. excruciatus* Moser.

Subgenus **Cortinarius** [*Agaricus* subgenus *Inoloma* (Fr.) Loudon 1829]. Small to medium sized, more rarely large but always fleshy carpophores with dry, hygrophanous or non-hygrophanous pileus with frequently squamose-tomentose surface. Cuticle of pileus formed by hyphae (8)-10-15  $\mu\text{m}$  broad. Spores subglobose to slightly elongate to broadly amygdaliform. Cheilo- and pleurocystidia and sometimes pilocystidia present. Pigment violet (vacuolar), olive green, or yellow to yellowish-brown; KOH provokes a red reaction.

*Type species:* *C. violaceus* (L. ex Fr.) Fr.

Sect. 36. **CORTINARIUS** (*Agaricus* sect. *Inoloma* Chev. 1826). Pigment violet, vacuolar. Cuticle of pileus tomentose and squamose. Spores subglobose or broadly almond-shaped.

*Type species:* *C. violaceus* (L. ex Fr.) Fr.

*C. violaceus* (L. ex Fr.) Fr.; *C. hercynicus* (Pers. ex) Moser.\*

*Note:* A number of further species referable to subgenus *Cortinarius* occurs in the Pacific area from Japan to New Zealand, in the Western United States.

\*Also *C. kerrii* Sing. in Sing. & Araujo. - R.S.

*Pilze*, p. 87. 1877.

by M. Moser

*Type species: D. cinnamomea* (L. ex Fr.) Wünsche.Syn.: *Agaricus* (ser. *Cortinaria*) trib. *Dermocybe* Fr., *Syst. Myc.* 1: 227. 1821.  
*Cortinarius* trib. *Dermocybe* (Fr.) Fr., *Epicr.* p. 283. 1838.

**Characters:** Carpophores small to medium sized, with not (or indistinctly) hygrophanous, glutinous or dry pileus, young globose to semiglobate or campanulate, naked to fibrillose and slightly scaly; lamellae yellow, green, orange, yellow-brown, or red; stipe generally concolorous with the young lamellae, cylindrical to slightly clavate; universal veil weakly to strongly developed, either concolorous or different in color as compared with the cortina; context pigmented; taste often more or less bitter. KOH on context reacting red, dark brown or black; spores elliptical to pip-shaped, rarely subglobose or ± lemon-shaped, generally not more than 10 µm (exceptionally up to 13 µm) long; clamp connections present; all species rich in anthraquinonic pigments.

**Development of the carpophores:** Bivelangiocarpous and stipitocarpous.

**Area:** Mainly in the temperate zone of the Northern Hemisphere, only one subgenus in the *Nothofagus*-area of the Southern Hemisphere.

**Limits:** Aside from the macroscopical and anatomical characters indicated in the generic diagnosis, the principal condition for admission of a cortinariaceous species in *Dermocybe* is now the presence or absence of certain anthrachinonic pigments some of which appear to be characteristic for and exclusive in *Dermocybe*. For nearly all species of subgenus *Dermocybe*, six pigments are characteristic: endocrocin, dermorubin, dermolutein and three less well defined pigments "no. 20, 22, 23"); in addition to these some other pigments: fallacinol, erythroglauclin, cinnarubin, cinnalutein, flavomannin-6,6-dimethyl ether, emodin/emodin-glycosid and physcion (for more detail see Gruber, *Zeitschr. Pilzk.* 36: 95-112, 1970) are found in Dermocytes. The presence of endocrocin is characteristic and diagnostic for all Dermocytes.\*

**State of knowledge:** The former subgenus *Dermocybe* has now been considerably constricted and emended, and contains nearly fifty species, 39 of which are here enumerated.

**Practical importance:** Most species of *Dermocybe* are obviously ectotrophically mycorrhizal, but some of them may be only facultatively mycorrhizal (ectotroph-formers) and as such of importance in forestry. It is not fully established whether in *Dermocybe*, as delimited at present, species with poisonous substances actually occur. *Cortinarius orellanus* has been removed from the genus. It is however possible that some true Dermocytes are poisonous.\*\*

\*For further precision with regard to the pigment-chemical data on the European species of *Dermocybe* see also the recent work of G. Keller, *Sydowia* 35: 110-126. 1982. R.S.

\*\*This occurs because of the laxative action of anthraquinones (Bresinsky & Besl). - R.S.

## SPECIES

Subgenus **Icterinula** Moser & Horak. Lamellae and/or stipe yellow orange, yellow-brown, olivaceous; pileus often the same color as lamellae and stipe, dry to viscid or even glutinous. Yellow anthraquinonic pigments occurring; there are also indistinct traces of a red pigment (which might be cinnarubin or a pigment chemically related to it); yellow pigments are endocrocin, in some species dermolutein (?) and several not defined pigments. Under *Nothofagus* in the Southern Hemisphere.

*Type species:* *D. amoena* Moser & Horak.

Sect. 1. **ICTERINULA** Moser & Horak. Characters of the subgenus.

*Type species:* *D. amoena* Moser & Horak.

Stirps *Amoena*. (Pileus membranous to thin-fleshy, transparently striate, with yellow colors and slightly gelatinized epicutis; stipe slender.)

*D. amoena* Moser & Horak; *D. icterina* Horak; *D. heterochroma* Moser.

Stirps *Nothoveneta*. (With predominantly olivaceous or yellow - with olivaceous hue - colors; small to medium sized, fleshy, only weakly striate, without gelatinization in the epicutis, or with a very weak one.)

*D. nothoveneta*; *D. austronanceiensis* Moser; *D. chrysopthalma* Moser; *D. olivaceoicterina* Moser.

Stirps *Olivaceobubalina*. (Smaller carpophores with membranous to thin-fleshy pileus, with ± brown to olivaceous colors; stipe concolorous; lamellae olive yellow at least in young specimens; epicutis not gelatinized.)

*D. olivaceobubalina* Moser; *D. semipellucida* Moser; *D. gomphocystis* Moser.

Sect. 2. **PAUPERAE** Moser. Pileus dry to subviscid; carpophores yellow, yellow-brown, olivaceous. Yellowish pigment turning wine red with magnesium acetate. A bright pink fluorescent substance visible in ultraviolet light.

*Type species:* *D. luteostriatula* Moser & Horak.

Stirps *Luteostriatula*. (Small carpophores with membranous, transparently striate pileus; colors brown and yellow; surface when humid, somewhat viscidulous but no gelatinous layer observed in the epicutis.)

*D. luteostriatula* Moser; *D. flavofucata* Horak & Moser.

Stirps *Austroveneta*. (Small to medium sized carpophores with predominantly olive green colors in addition to yellow and brown ones, not or only slightly striate, fleshy, dry to subviscid, but without gelatinized layer.)

*D. austroveneta* (Cleland) Moser; *D. olivipes* Moser; *D. obscuroolivea* Moser (with var. *brunnea* Moser); *D. hypoxantha* Moser; *D. alcalisensibilis* Moser.

Subgenus **Dermocybe**. Pileus dry, not or rarely hygrophanous, with yellow, green, or red colors on lamellae and stipe and often also on pileus. In addition to endocrocine, and dermolutein mostly red pigments (dermorubin, dermocycin, cinnarubin, or several of these at the same time) present.

Type species: *D. cinnamomea* (L. ex Fr.) Wünsche.

Sect. 3. *HOLOXANTHAE* Moser. With endocrocin and traces of dermolutein, without dermorubin but sometimes with traces of two red or pink pigments (5-Cl-dermorubin?, and an unidentified pigment).

Type species: *D. holoxantha* Gruber & Moser.

*D. holoxantha* Gruber & Moser; *D. carpineti* Moser (ined.) (?*C. olivaceofuscus* Kühn.; ?? *C. schaefferi* Bres.); *D. alnophila* Moser; *D. sphagnogena* Moser.

Sect. 4. *DERMOCYBE*. With yellow orange, olivaceous (pileus often brown) colors, but pigment analysis shows dermorubin in addition to yellow pigments; all species containing flavomannin-6.6'-dimethyl ether.

Type species: *D. cinnamomea* (L. ex Fr.) Wünsche.

Stirps *Palustris*. (Mostly between *Sphagnum* in bogs; lamellae and stipe olive green at least when young; with or without a well developed veil.)

*D. palustris* (Moser) Moser with var. *palustris* and var. *sphagneti* (Orton) Moser.

Stirps *Cinnamomeus*. (Without olive green colors in the lamellae and without red veil; most frequently not among *Sphagnum*.)

*D. cinnamomeolutea* (Orton) Moser with var. *cinnamomeolutea* and var. *porphyreovelata* Moser; *D. bataillei* (Favre) Moser (ined. - *C. bataillei* Favre nom. subnud.); *D. cinnamomeobadia* (Henry) Moser; *D. crocea* (Schaeff. ex Fr.); *D. croceifolia* (Peck) Moser; *D. aureifolia* (Peck) Moser; *D. cinnamomea* (L. ex Fr.) Wünsche.

Stirps *Uliginosus*. (With reddish veil; growing with *Salix* and often among *Sphagnum*.)

*D. uliginosa* (Berk.) Moser (*C. concinnus* Karst; *C. queletii* Bat.; *C. orellanus* Fr. sensu Quél., Boud. non al.).

Sect. 5. *MALICORIAE* Moser. Characters of sect. *Dermocybe* but without flavomannin-2.2'-dimethyl ether.

Type and only species known: *D. malicoria* (Fr.) Ricken (*D. croceifolia* (Peck) Moser sensu Moser 1953, 1955).

Sect. 6. *SANGUINEAE* Kühn. & Romagnesi ex Moser. Species with red lamellae, often also red veil; stipe and often pileus likewise red; dermocycin, dermorubin, dermolutein or cinnarubin and cinnalutein respectively present; flavomannin-6.6'-dimethyl ether absent.

Type species: *D. sanguinea* (Wulf. ex Fr.) Wünsche.

Stirps *Semisanguinea*. (Only lamellae and in some species veil red; emodin absent; contains a substance showing blue fluorescence under ultraviolet light.)

*D. semisanguinea* (Fr.) Moser in Gams; *D. pallidipes* Moser; *D. phoenicea* (Bull. ex Maire) Moser with var. *phoenicea* and var. *occidentalis* A.H. Smith.

*Stirps Cinnbarina*. (In all parts - red; pileus hygrophanous; with cinnarubin and cinnalutein (instead of dermorubin and dermolutein.)

*D. cinnabarina* (Fr.) Wünsche.

*Stirps Anthracina*. (Pileus hygrophanous, brown; lamellae, stipe, and margin of the pileus carmine red in young specimens; only with anthraquinon-carbonic acids.)

*D. anthracina* (Fr.) Ricken (sensu Fr. non Ricken; *C. anthracinus* var. *purpureobadius* Karst.).

*Stirps Atropurpurea*. (Context of stipe wine red; pileus and veil also wine red. Under *Nothofagus* in South America.)

*D. atropurpurea* Horak.

## 175. LEUCOCORTINARIUS (Lange) Sing.

*Lloydia* 8: 141. 1945.

*Type species: Cortinarius bulbiger* (A. & S. ex Fr.) Lange.

*Syn.: Cortinarius* subgenus *Leucocortinarius* Lange, *Dansk. Bot. Ark.* 8(7): 6. 1935.

*Cortinellus* Roze sensu Konr. & Maubl. *Icon. Sel Fung.* 6: 146. 1924-37 non sensu Karst. (1879) nec sensu originali.

*Characters:* Those of *Cortinarius*, subgenus *Phlegmacium* sect. *Scauri* but spore print whitish, by dehydration soon light ochraceous and spores smooth; cuticle of the pileus consisting of interwoven hyphae which become more parallel in the epicutis; pigment concentrated in the hypodermium, intracellular, or at least not incrusting the walls of the hyphae; pileus neither distinctly viscid nor hygrophanous; lamellae truncato-emarginate; veil - a thick cortina or a thin subcortinoid annulus; hymenophoral trama regular; spores under the microscope hyaline, rather thick-walled (wall 0.5-1.0  $\mu\text{m}$  thick), wall not distinctly double, without callus or germ pore, inamyloid, smooth, cyanophilic, binucleate; hyphae of the trama of the context interwoven, inamyloid, with clamp connections. On the earth in woods. earth in woods.

*Development of the carpophores:* Bivelangiocarpous and pileocarpous with a universal veil with double structure, no such duplex structure has been observed in *Derocybe uliginosa*, but it does exist in *Cortinarius*, e. gr. *C. calochrous* (Reijnders).

*Area:* Europe.

*Limits:* This genus differs from *Tricholoma* (Tricholomataceae) in the somewhat thick-walled, ochraceous spores, the cortina connecting the bulb with the margin of the pileus, the presence of clamp connections, which, in Tricholomas with even a trace of cortina, are always constantly absent. *Leucocortinarius* differs from *Tricholomopsis* (Tricholomataceae) in the absence of cheilocystidia and in the presence of a bulb at the base of the stipe, also in more elongated spores and the color of the spore print. These differences would amply justify the generic separation of this genus from all similar forms in the Tricholomataceae but it is highly questionable

whether they in themselves would be enough to remove *Leucocortinarius* from the Tricholomataceae to Cortinariaceae as has been done by Konrad & Maublanc and by Lange. Lange even went one step further and considered *Leucocortinarius* as a subgenus of *Cortinarius*, an arrangement which the author thinks goes too far.

The author has, however, become convinced that Konrad & Maublanc and Lange were right in considering *Leucocortinarius* as belonging to the Cortinariaceae rather than the Tricholomataceae because the spores of *Leucocortinarius bulbiger* are bi-nucleate whereas in all tricholomataceous genera similar and comparable to *Leucocortinarius* they are uni-nucleate. The fresh spore print is near Romagnesi Ib.

*State of knowledge:* Only one or two species are known.

*Practical importance:* The genus may be of some importance in forestry (as ectotrophically mycorrhizal fungi).

## SPECIES

*L. bulbiger* (A. & S. ex Fr.) Sing. (*Armillaria*, Kummer; *Tricholoma*, Ricken; *Cortinellus*, Gillet; *Cortinarius*, Lange); apparently also *Armillariella castulifera* Romagnesi (with more membranous veil).

### 176. STEPHANOPUS Moser & Horak

*Nova Hedw.*, Beih. 52: 520. 1975.

*Type species:* *Stephanopus azureus* Moser & Horak.

*Characters:* Carpophores fleshy and large, with the habit of a *Stropharia*; pileus glutinous; stipe with a membranous annulus which is sulcate on the upper side, below the annulus with several incomplete floccose belts from the universal veil; carpophores in all parts with bright blue or violet pigments; spores lemon-shaped, strongly verrucose, with a well delimited plage; cheilo- and pleurocystidia present, clavate, filiform or lageniform, often with a slender, filiform appendage; clamp connections present; hymenophoral trama regular; spore print ferruginous. On humus in woods of *Nothofagus*.

*Development of the carpophores:* Not studied in detail.

*Area:* *Nothofagus*-zone of temperate South America.

*Limits:* The similarity with *Stropharia* sect. *Stropharia* and the spore morphology are characteristic; the genus is certainly close to *Rozites* and *Cortinarius* but differs in the well developed plage of the spores and the type of cystidia.

*State of knowledge:* Three species have been described in the genus.

*Practical importance:* Unknown; but probably ectomycorrhizal.

## SPECIES

*S. azureus* Moser & Horak; *S. caeruleus* (Moser) Horak ("caerulea"); *S. stropharioides* Horak apud Moser & Horak. Horak now thinks that *C. trachyploeus* Moser & Horak belongs in this genus rather than *Cortinarius* (see also p. 628).

### 177. GYMNOPILUS Karst.

Hattsv., *Bidr. Finl. Nat. Folk* 32: xxi. 1879.

Type species: *G. liquiritiae* (Pers. ex Fr.) Karst.

Syn.: *Ryssospora* Fayod, *Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 361. 1889.\*  
*Fulvidula* Romagnesi, *Rev. d. Mycol.* 1: 209. 1936 (not validly published).

**Characters:** Pileus usually bright colored mostly bright yellow, fulvous, red, blue, lilac, green, etc., some pigments incrusting the hyphal walls, viscid or hygrophanous or dry, glabrous, fibrillose, squamulose, squarrose, floccose, or rimose; epicutis formed by the hyphal chains which are frequently erect, forming some kind of a trichodermium, at least in the center of the pileus, and then the terminal members often assuming the character of dermatocystidia (e. gr. in *G. zenkeri*), always incrusted by the pigment; lamellae adnexed to decurrent, narrow to broad, becoming very brightly and richly rusty in dried mature carpophores; spore print very brightly and richly ferruginous-fulvous, e. gr. "amber brown" with a slight shade of "Argus brown", or between "vinaceous orange" and "Mars orange", or brighter than "vinaceous russet" and "ferruginous" (Ridgway), between Pl. 4, A 12 and Pl. 11, A 12 or near "Arab" (Maerz & Paul); spores under the microscope usually well colored, rusty-melleous, with double wall, without germ pore, ellipsoid, short-ellipsoid, or amygdaloid-ellipsoid, distinctly warty when seen in ammoniacal medium under an oil immersion lens and focussed upon the upper surface (rather than in optical section); very frequently pseudoamyloid in freshly dried prints, ornamentation exosporial and rarely projecting more than 0.6  $\mu\text{m}$ ; most lignicolous species with broad refringent acid-insoluble crystals in the lamellae; basidia without siderophilous granulation, and either clavate or constricted between an apical capitate part and the lower ventricose part, or else ampullaceous, 4-spored or 2-spored; cystidia always present on the edge of the lamellae and in its neighborhood (cheilocystidia), sometimes a similar type of cystidia found all over the sides of the lamellae, and then often strongly incrusted with resinous pigment matter; cheilocystidia usually ventricose below, and the tapering apex often again thickened to a subcapitate tip, small to medium sized, scattered among the basidia or making the edge

\*I have given (Singer 1961) a detailed account why Singer & Smith (1946) have selected "*Flammula apicrea* (Fr.) Gillet" as the type species of *Ryssospora* and this typification has been accepted by other mycologists even though Fayod's generic description is not very precise and other species named by him (*Pholiota mustelina* sensu Fayod - G - is a *Galerina* of the stirps *Marginata*) seem to show that he did not distinguish *Galerina* properly, nor was *Phaeocollybia* well distinguished if we may assume that his *Naucoria hilaris* is this species in the modern sense. Horak (1968) concludes that still existing sketches of *F. apicrea* sensu Fayod clearly demonstrate that it belongs in *Gymnopilus*. This was confirmed by my own revision of this material at G.

heteromorphous; hymenophoral trama regular; trama, subhymenium and hymenial elements very frequently dyed uniformly deep and rich yellow because of a soluble ( $\text{NH}_4\text{OH}$ ) intercellular (?) pigment permeating the preparation, consequently the hyphae becoming frankly green when dyed with some blues, e. gr. cotton blue C<sub>4</sub>B according to Romagnesi (but it is not clear whether this behavior is also noticeable in the few species without yellow soluble pigment); stipe usually yellow or almost so, never considerably or constantly eccentric and always nearly as long as the diameter of the pileus or longer, well developed and not bulbous-marginate, nor constantly strongly curved and thus touching the margin of the pileus, often with a distinct (cortinoid to membranous) veil which in some species appears as a well developed annulus, always annulate if the pileus is viscid, never showing a distinct pseudorhiza but sometimes inserted in the wooden substratum; context often bitter; all hyphae with clamp connections. On coniferous wood, or on frondose wood, on dead palms, on living orchids, on grass roots, etc., rarely on foliage or other debris. Not ectotrophically mycorrhizal but some species endotrophically mycorrhizal with orchids (Pl. 1,1). KOH staining the surfaces dark (deep chestnut to black), at least in most species, especially where the surfaces have been dusted by discharged spores.

*Development of the carpophores:* Monovelangiocarpous (*G. sapineus*) or paravelangiocarpous, almost gymnangiocarpous; stipitocarpous (Reijnders).

*Area:* Almost cosmopolitan (except in the Antarctic continent), but less well represented outside the forested areas.

*Limits:* The distinctly ornamented spores distinguish *Gymnopilus* from *Pholiota* and indeed all genera of the Pholiotoideae (Strophariaceae). The EM structure of the spore wall is the same as in other genera of the Cortinarieae (cf. Cléménçon 1973). Kühner (1978) while recognizing the similarity of *Gymnopilus* with *Cortinarius* thinks that the pigmentation of the former, because of the presence in some species of bisnoryangonine and hispidine tends to support the idea of affinity with *Pholiota*. While we give much importance to chemotaxonomical arguments it must be stated that too few species of *Gymnopilus* and none of *Pyrrhoglossum* have been analyzed to come to a positive conclusion. Such violet pigments as those of *Gymnopilus janthinosarx*, *G. calobasis*, *Pyrrhoglossum lilacipes* and *P. lilacinum* are likely to be similar or identical to the corresponding intracellular violet pigments of *Cortinarius*. The veil where developed in *Gymnopilus* is usually cortiniform, but the fibrils may be dense enough to produce a rather persistent annulus which, however, is somewhat different in structure from the often gelatinizing, membranous annulus of *Pholiota*. While this difference is not necessarily constant, it indicated the similarity of veil characters in *Cortinarius* and *Gymnopilus*. The latter differs from the former in cystidial characters and the total absence of any ectotrophic mycorrhiza formation.

The genus *Gymnopilus* comes closest to *Pyrrhoglossum*. It appears that the best way of separating these genera is given by considering as *Pyrrhoglossum* only those species that strictly correspond to all diagnostic characters of the latter rather than by separating species with just inconsistently slightly eccentric stipes from *Gymnopilus* species which are otherwise closely related.

Some species of *Gymnopilus* have not only the habit of the fleshier species of *Galerina* but show a plague in a minority of spores or a very small or dislocated one in many spores. These species, such as *G. cucumis* and related forms, have pseudoamyloid spores and could easily be taken for *Galerina* subgenus *Galerina*. Kühner (1978) discusses the similarity of the spores of *Galerina* and *Gymnopilus* and, as far as I can interpret his results, he seems to rely mainly on pigment chemistry in order to separate the two genera since styrylpyrones and derivatives have been observed in several species of European Gymnopili, but not in *Galerina sphagnorum*. He adds that, evidently, "it would be very imprudent to draw the conclusion from these all too rare analyses that the absence of such pigments is a general characteristic of the "Tubarieae" [i.e. *Galerina* and, according to Kühner, related groups excluding *Gymnopilus*]. Also the frequent strong reaction of the carpophores with KOH in *Gymnopilus*, not observed in similar Galerinas, is not fully constant and applicable to all species of *Gymnopilus*.

Thus we have several characters (plage, pigment chemistry, habit), none of them by itself very sharp and absolutely decisive, but when taken in connection with the obvious affinities of the respective species, as a whole quite serviceable to distinguish *Gymnopilus* from *Galerina*, not, however, sufficient to classify each of these genera in a different tribus or family.

*State of knowledge:* After some special studies devoted to this genus - recently by a monograph by Hesler (*Mycologia Memoir* no. 3, 1969) who distinguished 73 species, and a thorough study of the Amazonian species (still unpublished) by I. Araujo Aguiar - the genus may be considered to be rather well known. It should be noted, however, that the pseudoamyloid reaction of the spores, emphasized by Hesler, should be used with caution since older dried specimens have a tendency to lose the pseudoamyloidity. In the enumeration of the species below I recognize definitively only the 78 species known to me personally.

*Practical importance:* Many species are mild wood destroyers though they rarely infect freshly cut lumber. Some species may be used in horticulture since they form orchid mycorrhiza. The yellow soluble pigment of many species can be used for dying material for cytological studies. *G. purpuratus* and *P. aeruginosus* contain an alkaloid which is said to have psychotropic effects and the surfaces of the carpophores turn blue or green as in the hallucinogenic *Psilocybes*. At the same time, more than one species (for example *G. spectabilis*, *G. depresso*) are eaten in certain regions in spite of their more or less bitterish taste, without ever producing any hallucinogenic effect. It seems to me that where *G. spectabilis* has been reported as having "psychotropic" qualities, the respective collections have been misidentified (see also Singer in Rumack & Salzman, *Mushroom Poisoning ...* 1978, p. 212).

There is no doubt but that poisonous species do exist. We have observed a species, apparently identical or close to *G. spadiceus* Romagn., which gave us a positive Meixner reaction. The specimens (WU) came from the Schwarzalm Moor bei Göstling, N-Ö, Austria. I am convinced that this is not the only species of the genus that should be suspected of containing amanitins.

## SPECIES

Sect. 1. *ANNULATI* [Romagnesi (1942)] Sing (*Gymnopilus* subgenus *Annulati* Hesler, l.c. p. 18, 1969). Membranous annulus persistent or cortina abundantly developed so as to form a distinct annular zone.

Type species: *G. spectabilis* (Fr.) Sing.

*G. janthinosarx* (Sing.) Sing.; *G. purpuratus* (Cooke & Mass.) Sing.; *G. luteofolius* (Peck) Sing.; *G. dilepis* (Berk. & Br.) Sacc.; *G. intermedius* (Sing.) Sing.; *G. aeruginosus* (Peck) Sing.; *G. spectabilis* (Fr.) Sing. (*Agaricus spectabilis* Fr. non Weinm.; *A. quercicola* Lasch; *Agaricus aureus* var. *truncicola* Kretschmar apud Klotzsch in Rab.); *G. armillatus* Murr.; *G. brittoniae* (Murr.) Sing.; *G. ventricosus* (Earle) Hesler; *G. pampeanus* (Speg.) Sing.; *G. suberis* (Maire) Sing. (the last four species may be considered subspecies of *G. spectabilis*); *G. aculeatus* (Bres. apud Roumeguère) Sing.; *G. peliolepis* (Speg.) Sing.; *G. braendlei* (Peck) Sing.; *G. pulchrifolius* (Peck) Murr.; *G. imperialis* (Speg.) Sing.; *G. oxylepis* (Berk. & Br.) Sing.; *G. filiceus* (Cooke) Sing.; *G. excentriciformis* Sing.; *G. crocias* (Berk. & Br.) Sing.; *G. hispidellus* Murr.; *G. chrysites* (Berk.) Sing.; *G. hispidus* (Mass.) Murr.; *G. trailii* (Berk. & Cooke) Sing.; *G. igapoensis* Araujo; *G. viaticus* Araujo; according to Hesler also *G. subspectabilis* Hesler; *G. fulvosquamulosus* Hesler; *G. validipes* (Peck) Hesler; *G. luteus* (Peck) Hesler; *G. palmicola* Murr. (said to be ferruginous to ochraceous and consequently not identical with *G. aculeatus*); *G. chrysenteroides* Murr.; *G. rufosquamulosus* Hesler; *G. pholiotoides* Murr.

Sect. 2. *GYMNOPILUS* (*Sapinei* Fr. ut sect. *Agarici* trib. *Flammula* = *Cortinatae* Romagnesi ut sect. *Fulvidulae*). Veil slight, not forming an annulus, often practically absent.

Type species: *G. sapineus* (Fr.) Maire.

*G. punctifolius* (Peck) Sing. (*G. subviridis* Murr.); *G. sapineus* (Fr.) Maire; *G. penetrans* (Fr. ex Fr.) Murr. (sensu Lange); *G. hybridus* (Fr. ex Fr.) Maire; *G. amarissimus* Murr.; *G. flavidellus* Murr.; *G. subdryophilus* Murr.; *G. liquiritiae* (Pers. ex Fr.) Karst.; *G. microsporus* Sing. (*Flammula liquiritiae* sensu Bres. \* non Fr.); *G. bellulus* (Peck) Murr. (Naucoria, Sacc., Fulvidula, Joss.); *G. picreus* (Fr.) Karst.; *G. alpinus* (Sing.) Sing.; *G. chilensis* Sing.; *G. tonkinensis* (Pat.) Sing.; *G. fulgens* (Favre & Maire) Sing.; *G. pratensis* Sing., *G. flavus* (Bres.) Sing. (Naucoria, Bres.; *Flammula dactylicola* Lange); *G. chrysopellus* Berk. & Curt.) Murr. (probably identical: *G. chrysotrichus* (Berk. & Curt.) Murr.); *G. geminellus* (Peck) Murr. (*G. subpenetrans* Murr.); *G. earlei* Murr. (*G. tenuis* Murr.); *G. depresso* Murr.; *G. zenkeri* (Henn.) Sing.; *G. praefloccosus* Murr. (possibly better in section 1); *G. marasmioides* (Berk.) Sing. (*Agaricus amazonicus* Berk.); *G. submarasmioides* Sing.; *G. microlopus* Sing.; *G. radicicola* Sing.; *G. macrosporus* (Sing.) Sing. (c.n. = *Pyrrhoglossum macrosporum* Sing., *Sydowia* Beih. 7: 92. 1973); *G. velutinus* (Petch) Sing. (c.n. = *Crepidotus velutinus* Petch, *Ann. R. Bot. Garden Peradeniya* 9: 225. 1924);

\*Bresadola, *Ic. Myc.* 783 has been cited as an illustration of *G. liquiritiae* by Hesler who quotes much larger spores in his description.

*G. holocrocinus* (Berk.) Sing. (c.n. = *Agaricus holocrocinus* Berk., *Hook. Lond. Journ. Bot.* 6: 485. 1847); *G. humicola* Harding ex Sing.; also some unpublished species from Amazonia: *G. violaceus*, *G. calobasis*, *G. campinaranae*, *G. gymnocheilus*, *G. austrofulgens*, *G. psammophilus*, *G. submicrolopus*, *G. mariae*, *G. naematolomatoides*, *G. cucumis* Araujo (all with pseudoamyloid spores and the following with inamyloid spores): *G. osmarinianus*, *G. subdepressus*, *G. galerinoides*, *G. singeri*, *G. jaimei*; *G. tricholomatoides*, *G. distans*, *G. inpae*, *G. terraefirmae*, *G. paraensis*, *G. galerelloccystis*, *G. heterocheilus* Araujo (in dissertation, University of Amazonas/INPA 1985). - According to Hesler also here: *G. underwoodii* (Peck.) Murr.; *G. terrestris* Hesler; *P. parvisquamulosus* Hesler; *G. sordidostipes* Hesler; *G. bryophilus* Murr.; *G. pacificus* Hesler; *G. lepidotus* Hesler; *G. subtropicus* Hesler; *G. obscurus* Hesler; *G. fulvicolor* Murr.; *G. parvulus* Murr.; *G. naucorioides* Hesler; *G. subbellulus* Hesler; *G. rufescens* Hesler; *G. dryophilus* Murr.; *G. praelaeticolor* Murr.; *G. luteoviridis* Thiers; *G. areolatus* Murr.; *G. rufo-brunneus* Hesler; *G. echinulisperus* Murr.; *G. mitis* Hesler; *G. melleus* Hesler; *G. subsapineus* Hesler; *G. aurantiophyllus* Hesler; *G. luteocarneus* Hesler; *G. oregonensis* Murr.; *G. croceoluteus* Hesler; *G. abramsii* Murr.; *G. angustifolius* Hesler; *G. arenicola* Hesler; *G. magnus* (Peck) Murr.; *G. fuscosquamulosus* Hesler; *G. aurantiacus* Hesler; *G. decurrents* Hesler; *G. lutescens* Hesler; *G. viridans* Murr. - According to Pegler also *G. baileyi* (Berk. & Br.) Pegler, *G. crociphyllus* (Cke & Mass.) Pegler and *G. purpureonitens* (Cke & Mass.) Pegler.

## 178. PYRRHOGLOSSUM Sing.

*Mycologia* 36: 367. 1944.

*Type species: Agaricus pyrrhus* Berk. & Curt.

*Characters:* Habit pleurotoid; pileus sublaterally or distinctly eccentrically attached, sometimes the stipe strongly reduced, or if present short and curved, epicutis of elongated, more or less repent hyphae but these may be ascendant in bunches to form a fibrillose or woolly covering, many of the epicuticular and/or hypodermial hyphae heavily incrusted and with an intraparietal pigment (chestnut to melleous); lamellae eventually becoming bright rusty colored; spore print bright rusty; spores mostly small (<6 µm), more rarely up to 8.5 µm (but then stipe not longer than 4 mm), distinctly verrucose from an exosporial ornamentation (in EM section typically of the *Cortinarius*-type, i.e. elevations irregularly hollow), without a well delimited plage (although suprahilar region sometimes less or not ornamented); basidia normal; cystidia generally none; cheilocystidia present (rarely scattered in the neighborhood of the heteromorphous edge), rarely pleurocystidia (like the cheilocystidia) also on the sides of the lamellae; hymenophoral trama regular, its hyphae not gelatinized; veil inconspicuous or none; hyphae with clamp connections, mostly exuding bright yellow dissolved pigment when mounted in KOH, on wood. Surfaces staining dark with KOH.

*Development of the carpophores:* Not studied in detail but at least in one species "hemiangiocarpous".

**Area:** Tropics and subtropics, few species in warm-temperate climate; in America, Asia, and New Zealand.

**Limits:** The verrucose spores distinguish this genus from *Pleuroflammula*. The genus is well differentiated from *Gymnopilus* if care is taken to admit only species where the carpophore is at maturity strictly and consistently pleurotoid, and the spores are small except in very scantily or only eventually pigmented pilei and stipes. "Intermediate" forms, with larger spores or with only inconstantly eccentric (but usually broad) stipes like *G. macrosporus*, *G. velutinus*, and *G. holocrocinus* are closer to *Gymnopilus* and must be referred to this latter genus.

**State of knowledge:** Six species belonging here are well known.

**Practical importance:** Unknown.

## SPECIES

Sect. 1. *PYRRHOGLOSSUM*. Hyphae well pigmented by an intraparietal pigment, without any lilac pigments; spores small, more rarely large and then with high ornamentation.

**Type species:** *P. pyrrhus* (Berk. & Curt.) Sing.

*P. pyrrhus* (Berk. & Curt.) Sing. (*Crepidotus substipitatus* Murr.); *P. stipitatum* Sing.; *P. hepatizon* (Berk.) Dennis; *P. ferruginatum* (Lloyd) Sing. (*Crepidotus sarakawensis* Pilát).

Sect. 2. (Unnamed). Hyphae with lilac pigment at least in some parts of the carpophore; spores small.

*P. lilacipes* Sing.; *P. lilacinum* Horak.

## 179. PHAEOCOLLYBIA Heim

Genre Inocybe, p. 70. 1931.

**Type species:** *Naucoria festiva* (Fr.) Bres.

**Characters:** Habit collybioid; pileus usually glabrous, humid, subviscid to viscid or glutinous, often acute, conical or campanulate, later expanding and often umbo-nate; epicutis consisting of repent, filamentous hyphae which are mostly more or less gelatinized; lamellae subfree to adnexed, becoming rusty brown to deep and rich cinnamon in age, with paler or pallid edge (under a lens); spore print rusty to ochraceous brown; spores rusty to rusty-melleous (more rusty in KOH if strongly warty, more melleous when ornamentation is very low); verrucose or punctate, sometimes very weakly so but never quite smooth i.e. not completely devoid of exosporial ornamentation, sometimes with a rather persistent smooth perispore which, in light microscopy may cause an effect as in ornamentation type XI but spore wall struc-

ture in EM sections typically cortinarioid), without a well delimited suprahilar plage\*, inamyloid or pseudoamyloid, without germ pore, but often with a mucro-like apical knob which may have differentiated wall material (being less pigmented or ornamented) and these spores therefore have a callus, in few species a variable number of spores have a true germ pore, exceptionally even a truncate one, shape often characteristically mucronate-beaked, but not always so, otherwise ellipsoid to ovoid-subamygdaliform; basidia normal (but bisporous forms exist); cystidia none or scattered and then like the cheilocystidia; cheilocystidia present, narrow, filamentous-capitate or clavate and broadened to 4-9  $\mu\text{m}$  above, or else ventricose or subcylindric with narrowed neck which is frequently colored and refractive (in KOH), making the edge more or less heteromorphous; hymenophoral trama regular with densely packed subparallel hyphae; stipe cartilaginous but often fragile, especially in dried condition, innately striate-fibrillose or more frequently quite smooth, viscid or dry pseudorrhiza more or less developed and often very conspicuous (Pl. 44); veil rudimentary, pruinose, practically absent even in young specimens; hyphae with or without clamp connections. On earth and humus mostly in coniferous woods and possibly rising from some buried vegetable matter which is reached by the pseudorrhiza.

*Development of the carpophores:* Unknown.

*Area:* Temperate zone (circumpolar), but also several tropical and New Zealand species.

*Limits:* The absence of a cortina and the characters of the stipe separate this genus from *Cortinarius*. In the latter genus, it would be looked for in *Phlegmacium* or *Myxacium*. *Phaeocollybia* differs from *Gymnopilus* in the combination of a glabrous, often hygrophanous and/or viscid pileus and an evelate stipe, or else in the absence of clamp connections, in the more developed pseudorrhiza, the less brightly rusty color of the spore print, or the narrowly adnexed to subfree lamellae. It differs from *Galerina* in the combination of clamped hyphae and spores without plage, or in the colors and habit as far as clamp-less species are concerned.

The genus is quite natural and rather easy to delimit from other genera of the Cortinarieae. The ornamentation of the spores is constantly present, at least in the great majority of the mature spores of a spore print. But care should be taken to observe the spores carefully in oil immersion since in some species the ornamentation may easily escape the inattentive observer. Species without a trace of a pseudorrhiza such as *P. odorata* Horak, and *Marasmius primulinus* Berk. do not seem to belong in *Phaeocollybia*. I suspect that they belong in *Galerina*.

*State of knowledge:* Thanks to recent studies by Heim, A.H. Smith, Bresinsky, Horak, Singer and Izonete Araujo Aguiar (the latter in a still unpublished thesis), the species belonging in this genus are reasonably well known. Of these I enumerate their respective sections with 20 species with which I am personally acquainted.

\*Horak (1977) illustrates spores with plage in species of *Phaeocollybia*. Even in specimens studied by both Horak and myself I was unable to recognize a true suprahilar delimited plage comparable with the plage of *Galerina*. For example *P. similis*, holotype, has no such plage (no. 12690 W, WU); it does have clamp connections.

*Practical importance:* Unknown. According to the ecological observations by the present author, the species of *Phaeocollybia* are not obligatorily ectomycorrhizal.

## SPECIES

Sect. 1. *SUBATTENUATAE* Sing. (1970). Cheilocystidia often subcapitate but versiform; spores  $>6.5\text{ }\mu\text{m}$ ; clamp connections present. Mostly tropical and subtropical.

*Type species:* *P. subattenuata* Sing.

*P. subattenuata* Sing.; *P. amazonica* Sing.; *P. brasiliensis* Araujo ined.; *P. elaeophylla* Sing. ined.; *P. megalospora* Araujo ined.; *P. oligoporpa* Sing. ined.; *P. similis* (Bres.) Sing.

Sect. 2. *RADICATAE* Sing. (1970). Cheilocystidia subcapitate or capitate; spores  $<6.5\text{ }\mu\text{m}$ ; clamp connections present.

*Type species:* *P. radicata* (Murr.) Sing.

*P. radicata* (Murr.) Sing.; *P. arduennensis* Bon; *P. flava* Araujo ined.; *P. cidaris* (Fr.) Romagnesi (sensu Karst., Horak).

Sect. 3. *VERSICOLORES* A.H. Smith (1957). Cheilocystidia attenuated to subacute and often capitate at apex; spores  $<6.5\text{ }\mu\text{m}$ ; clamp connections absent.

*Type species:* *P. lugubris* (Fr.) Heim.

*P. lugubris* (Fr.) Heim; *P. columbiana* Sing.; *P. cidaris* (Fr. sensu Karst.) Romagn.; obviously also *P. californica* A.H. Smith; *P. spoliata* Horak, *P. mexicana* Horak.

Sect. 4. *PHAEOCOLLYBIA*. Cheilocystidia in their majority clavate to  $\pm$  cylindrical; spores  $<6.5\text{ }\mu\text{m}$ ; clamp connections absent. Mostly North-temperate species of coniferous forests, more rarely in fagaceous forests (including those of the tropical-montane zone).

*Type species:* *P. festiva* (Fr.) Heim ex Sing.

*P. festiva* (Fr.) Heim ex Sing.; *P. christinae* (Fr.) Heim (*P. hilaris* (Fr.) Romagn. sensu Ricken; *P. lateria* A.H. Smith\*); *P. kauffmanii* (A.H. Smith) Sing.; *P. neosimilis* Sing. st. & n. nov. (*P. attenuata* ssp. *mexicana* Sing. *Sydotwia* 11: 367. 1957; *P. similis* sensu A.H. Smith non al.); *P. quercetorum* Sing. ined.; obviously also *P. fallax* A.H. Smith; *P. lilacifolia* A.H. Smith; *P. olivacea* A.H. Smith; apparently here: *P. muscicolor* Horak.

\*It is difficult to decide whether the original *A. hilaris* Fr. corresponds to *N. hilaris* sensu Ricken or to *P. hilaris* sensu Horak. Neither is based on authentic or topotypical material, but they are different from each other. Ricken's is certainly the first identifiable interpretation but Horak's is here preferred since Ricken's interpretation keys out with *P. christinae* (Fr.) Heim of Horak's key which is based among other materials on Swedish collections. It is improbable that Fries used the same species to be named twice. Besides *A. hilaris* was described without mention of the radicant base (but so was *A. christinae*).

Sect. 5. *MICROSPORAE* Sing. (1970). Cheilocystidia rather variable, often clavate to cylindrical as in sect. 4; spores <6.5  $\mu\text{m}$ ; clamp connections absent.

*Type species: P. christinae* (Fr.) Heim sensu Heim (= *P. jennyi* (Karst.) Heim).

*P. jennyi* (Karst.) Heim (often incorrectly spelled *jenniae*); seemingly also *P. sipei* A.H. Smith (as described, but conspecific with *P. californica* A.H. Smith (sect. 3); *P. rancida* Horak; *P. ratticauda* Horak; *P. corneri* Horak.

## 180. **GALERINA** Earle

*Bull. N. Y. Bot. Garden* 5: 423. 1909.

*Type species: Agaricus vittaeformis* Fr. (Epicrisis).

*Syn.: Galera* Kummer, *Führ. Pilzk.* p. 74. 1871 non Blume (1825).

*Galera* (Fr.) Quél., *Champ. Jura Vosg.* p. 135. 1871-2, non Blume (1825).

*Agaricus* tribus *Galera*, Fr. *Syst. Mycol.* 1: 264. 1821.

*Velomyces* Pilát, *Schweiz. Zeitschr. Pilzk.* 31: 172. 1953.

*Phaeogalera* Kühner, *Bull. Soc. Myc. Fr.* 88: 151. 1972.

*Characters:* Habit usually mycenoid, but sometimes collybioid or almost omphalioid and sometimes fleshier than usual and with well developed veil (these forms have formerly been mistaken for *Pholiota*); pileus usually more or less hygrophanous usually campanulate or conical in the early stages, but occasionally also semiglobose or subglobose, with an epicutis of strictly repent hyphae (some may at places have suberect ends but no palisade or hymenium is ever formed); dermatocystidia rare on the pileus, usually absent, if present, not forming a dense subhymeniform layer, globose cells none in the cuticle; pigment incrusting, melleous to brownish chestnut, tawny, ochraceous, more rarely orange brown, cinnamon or umber; lamellae adnexed to decurrent, usually white fringed; spore print more or less richly rusty in color (e. gr. "Alamo" or between "rust sorolla" and "Peruvian br.", Maerz & Paul), more rarely more tobacco brown; spores under the microscope melleous to rusty-fulvous, often rather pale colored in water or chloral hydrate but generally more deeply rusty in alkalis especially KOH, rarely smooth, usually with some kind of ornamentation which may be very low, or else very distinct and projecting and then usually distinctly warty or in short ridges, sometimes the ornamentation supplemented or replaced by a perisporial loosening, i.e. "calyptate" (Pl. 12,2), the walls distinctly complex, without a broad germ pore but sometimes with a distinct callus or even with a narrow non-truncate or slightly or inconsistently truncate germ pore, with a plage (Pl. 15; 81; 82; 83,1) which is distinctly delimited in the suprahilar region of the spore or merely with a ragged line marking the plage, more rarely without a suprahilar plage (and then hyphae without clamp connections, otherwise clamp connections present in the trama at least on the broader hyphae); pseudoamyloid or more rarely inamyloid, never amyloid, medium sized or large; basidia normal but either 4-spored, or 2-spored (or mixed), also many monosporous and tri-sporous basidia observed in some species; cystidia often present, in some species constantly present on the sides of the lamellae, in others only cheilocystidia present, but the latter never absent; hymenophoral trama regular or subregular, not bilateral

in any sense; hymenopodium little developed; stipe with traces of a cortinoid veil, more rarely practically elevate, on the other hand often with a distinct annulus or an annular belt or belts and then varying from silky to membranous, white to yellow, rarely green; dermatocystidia on stipe numerous in a few species down below the middle of the stipe, but most frequently absent or limited to the apex. In moss beds, also in sphagnum, on all kinds of dead vegetable matter, herbaceous leaves, grasses, dead foliage and needles, on sandy earth or loam, humus, burned matter, dead branches, stumps, dead bark or living trees, logs, rocks, especially when moss-covered.

*Development of the carpophores:* Probably always monovelangiocarpous (according to Reijnders for *G. paludosa* and *G. unicolor*) and apparently generally stipitocarpous.

*Area:* Cosmopolitan including tropics and Antarctica.

*Limits:* The species with spores having a well delimited plage cannot be confused with any other genus. A weak plage is known to exist in some *Cortinarii* but these are so different in habit and anatomy (no cheilocystidia and/or cystidia of the *Galerina*-type) that there is no need for using physiological or ecological methods to separate them. Those species without a plage, however, should be examined carefully for the presence or absence of clamp connections in the hyphae of the trama. If clamp connections are present, the fungus in question should not be sought in *Galerina* and if they are absent, the fungus in question belongs possibly in some other genus (possibly *Cortinarius* where very few species without clamp connections have been found, or in *Phaeocollybia* - both amply different macroscopically).

Species with smooth spores and no trace of plage-line may however belong in *Galerina* if the spores are pseudoamyloid and pleurocystidia are present, or if the spores are large and with inconsistently truncate small germ pore and a non-gelatinized epicutis is present which consists of narrow, filamentous (up to 7 µm broad) hyphae forming a thin cutis. Should these conditions not be fulfilled - especially if lignicolous species are involved - *Pholiota* sect. *Flammula* and *Kuehneromyces* should be compared.

In one section of *Galerina* the epicutis has a structure somewhat like that of *Phaeomarasmius*, but in this section pleurocystidia are differentiated, or a faint to rugged line marks off the spore-plage (or both) which generally shows a distinct suprahilar depression or applanation.

In one section of *Galerina* there is an apical germ pore which however, is not as broad and truncate as in *Kuehneromyces*. This has led Hora (1960) to actually synonymize the European species of *Kuehneromyces* with *Galerina*, an attitude Smith and Singer considered as systematically wrong and phylogenetically doubtful and which has also been rejected by Pegler & Young (*Transact. Brit. Mycol. Soc.* 52: 495, 1959) on the basis of spore wall ultrastructure. The opposite approach was adopted by A.H. Smith & Hesler (1969) who synonymized *Kuehneromyces* with a genus of Strophariaceae - *Pholiota*! The species of sect. *Porospora* of *Galerina* have indeed as mentioned above larger spores than are known to occur in *Kuehneromyces* and/or a smaller germ pore and their habit and habitat is typically that of *Galerina*.

This has been rechecked for *G. nybergii*, a species which may be considered as approaching *Kuehneromyces*, but I am fully satisfied that it is generically different from *Kuehneromyces*.

*Phaeogalera* Kühner is based on *Agaricus stagninus* Fr. and the section *Porospora* Smith & Sing. "is the typical one of the genus". The genus is distinguished from *Galerina* Earle because of the spore color which is the same as in *Agrocybe*, the non-pseudoamyloid spores without a plage-line and the absence of an ornamentation as well as the presence of a truncate germ pore.

I do not wish, at this point, to reject the new taxon as unnecessary, but, with the present evidence at hand, its delimitation from *Galerina* is impossible to trace since the characters enumerated above are certainly not correlated. The same spore color is not found in all species of *Porospora* (e. gr. *G. nybergii*); nor are inamyloid spores restricted to smooth-spored Galerinas since section *Pseudotubaria* has pseudoamyloid spores; and *G. pseudobadipes* = *G. camerina* with often ± ornamented spores, has inamyloid spore walls, yet at the same time often a narrow germ pore. Some forms in sect. *Calyptrospora* (e. gr. *G. cerina* var. *nebularium*) have spores which are pseudoamyloid and either have or (a certain percentage) have not a germ pore. It would be interesting to obtain data on the individual development of species related to *G. stagnina*. If, as expected, it is monovelangiocarpous, it would fit in with the observations thus far available in *Galerina* as well as in other genera of Cortinariaceae, rather than with the supposedly related genera of Strophariaceae.

Kühner has later on treated *Phaeogalera* as a subgenus rather than a genus.

As long as a better separation of *Phaeogalera* from the rest of *Galerina* cannot be elaborated, and within the classification here proposed. *Phaeogalera* must be inserted in the synonymy list of *Galerina* Earle.

There is some difficulty mainly with a species published by us in *Galerina* and attributed - with some doubts on the part of the present writer - to sect. *Porospora* as a stirps of its own, *Latericia*. Here, *G. lateritia*, in spite of small spores (which might be difficult to distinguish from typical *Kuehneromyces*-spores), shows characters otherwise in line with those of *Galerina* and might be considered as the species most closely related to *Kuehneromyces*. The thin stipe, conic to campanulate pileus, the non-truncate germ pore and ventricose-capitate cheilocystidia are here considered to be valid arguments in favor of close relationship with other Galerinas. A second species, *G. subdecurrans* however, has the epicuticular characters of *Phaeomarasmius*, and would better be classified in that genus (inasmuch as we have had opportunity to demonstrate non-truncate germ pores in at least two species of otherwise typical *Phaeomarasmius* species whose position in *Galerina* or *Kuehneromyces* would be highly artificial) if it were not for the very faint ragged line delimiting the suprahilar area which we interpret as a plage. But, if at all, this species would lead to *Phaeomarasmius* rather than to *Kuehneromyces*.

While it is perfectly correct to state that the characters of certain species of sect. *Porospora* approach those of certain Strophariaceae, it is equally correct to state that such an approximation of characters does not necessarily mean affinity. If one takes into consideration the close affinity of *Kuehneromyces* with *Psilocybe* and of

*Psilocybe* with *Stropharia*, it does not appear to be farfetched to interpret this approximation of characters as convergence. There is nothing particularly strange or unique in such convergences of groups of fungi with similar spore color and biology, but it would take more convincing evidence than we have at present, to establish true and direct affinity between *Galerina* and *Kuehneromyces*, whereby one genus is supposed to have derived from the other, let alone their being taken as congeneric with each other. A similar convergence exists between *Phaeomarasmius* and *Pholiota*, yet, just as in the relationship between *Kuehneromyces* and *Galerina* it is a small number of rather marginal forms which approach each other (some Pholiotas lacking the otherwise characteristic pleurocystidia, and some *Phaeomarasmius* having an incomplete germ pore).

Finally, in sect. *Pseudotubaria*, there is at the same time an approximation of characters towards *Tubaria* and towards *Pholiota*. However, in this case, although the smooth spores and, to a certain degree, the habit of the species involved make a comparison with both genera possible, there is no reason whatsoever to assume affinity. The spore wall characters and the cystidial characters set them apart.

*State of knowledge:* The Galerinas may now be considered one of the most intensely studied groups of the agarics. In the present work I recognize 169 species. However, more species will be discovered in Asia and Africa. See Pl. 12,2; 15; 51,1-2,6; 81; 82; 83,1.

*Practical importance:* Some of the species may be of interest to the geobotanist and ecologist since they always occur in definite habitat patterns and are characteristic for a number of associations. e. gr. Sphagneta. One tropical species (*G. sulcipes*) and several extra tropical species (*G. venenata*, *G. autumnalis*, *G. marginata*, *G. beinrothii*, *G. fasciculata*) are poisonous. Tyler & Smith (*Mycologia* 55: 358-359. 1963) and Besl (*Zeitschr. Myk.* 47: 253-255. 1981) have shown that these contain amanitoxins (presumably  $\alpha$ - and  $\beta$ -amanitin) and are thus chemically related to the group of *Amanita phalloides* - a warning not to overstress the taxonomical significance of chemotaxonomy in the case of the fungus toxins. High amounts of thioctic acid as recommended by Kubička (see under *Amanita* p. 447) have given excellent results in a *G. marginata* poisoning treated in a hospital in Illinois (USA).

## SPECIES

Subgenus I. *Tubariopsis* (Kühner) Smith & Sing. (1957). Clamp connections on the hyphae completely absent in the carpophores but may be present at times between the last subhymenial cell and the basidium; spores with roughened suprahilar region (no delimited plage were present); pleurocystidia generally absent.

*Type species:* *Galerina graminea* (Velen.) Kühner [*G. laevis* (Pers.) Sing.].

*Galerina heterocystis* (Atk.) Sm. & Sing. [*Galerula*, Atk.; *Galera fragilis* var. *clavata* Velen.; *Galerina clavata* (Velen.) Kühn.; *Galera*, Kühner & Romagnesi]; *G. semilanceata* (Peck) Sm. & Sing.; *G. nexpensis* Sing.; *D. dimorphocystis* Sm. & Sing.; *G. laevis* (Pers.) Sing. [*Galerina graminea* (Velen.) Kühn.; *Galera*, Velen.]; *G. sub-*

*ceracea* Sm. & Sing.; *G. brunneimarginata* (Murr.) Sm. & Sing.; (*Naucoria*, Murr.); *G. nigripes* Sm. & Sing.; *G. pucarensis* Sing.; *G. berteroana* Sing.; *G. montivaga* Sing.; *G. sanctixaverii* Sing.; *G. praetervisa* Sing. in Smith & Sing.; *G. radicellicola* Sing. in Smith & Sing.; *G. machangaraensis* Sing.; *G. arctica* (Sing.) Nezdominiogo, apparently also *G. nasuta* (Kalchbr.) Pegler.

Subgenus II. **Galerina**. Clamp connections present (although in a few species not on all septa); spores with plage unless completely smooth.

Type species: *Galerina vittaeformis* (Fr.) Sing.

Sect. 1. *CALYPTROSPORA* Sm. & Sing. (1957). Hyphae with clamp connections; spores calyprate.

Type species: *G. sahleri* (Quél.) Favre sensu Favre.

Note: In this section are grouped species in which the outermost layer of the spore wall fits tightly over the spore except at the apicular end where it loosens to form blisters often visible as "ears", one on each side of the suprahilar region (plage) when the spore is seen in frontal view. Pleurocystidia are typically absent and the surface of the pileus is not fibrillose except sometimes from loose remainders of the white to yellowish veil. Kühner (since 1935) believes that this section is not different from the following and that the calyprate spores may indicate only forms of non-calyprate-spored Galerinas. We maintain that sect. 1 is a natural as well as practically convenient taxon if the world flora is considered.

Certain species of this section are very similar in appearance to the smaller *Corticarii* of subgenus *Telamonia*. These latter differ in spores which are never calyprate.

*G. odora* A.H. Smith; *G. turfosa* Sm. & Sing.; *G. anelligera* Sm. & Sing.; *G. cortinariooides* A.H. Smith; *G. sahleri* (Quél.) Favre (Galera, Quél.; Galera calyptrospora Kühner); *G. filiformis* Sm. & Sing.; *G. fallax* Sm. & Sing.; *G. subcerina* Sm. & Sing.; *G. evelata* (Sing.) Sm. & Sing. (*Galerina hypnorum* var. *evelata* Sing.); *G. acicola* Sm. & Sing.; *G. boliviiana* Sing. apud. Sm. & Sing.; *G. sphagnicola* (Atk.) Sing. (Galerula, Atk.); *G. payettensis* Sm. & Sing.; *G. cerina* Sm. & Sing. with numerous varieties; *G. sequoiae* Sing. ined.; *G. austrocalyprata* Sing.; *G. nubigena* Sing.; *G. calyprata* Orton; *G. antarctica* Sing. in Sing. & Corte; *G. meridionalis* Sing. & Cléménçon; *G. oinodes* (Berk. & Curt.) Sing.; *G. subarctica* Smith & Sing.; *G. psathyrelloides* A.H. Smith; *G. farinacea* A.H. Smith.

Sect. 2. *MYCENOPSIS* Sm. & Sing. (1957). Spores without even a narrow germ pore although sometimes with a slight callus; varying from distinctly ornamented to smooth, not calyprate, mostly with a distinct suprahilar plage; pleurocystidia none.

Type species: *G. mycenopsis* (Fr.) Kühner (sensu Kühner = *G. pumila* (Pers. ex Fr.) M. Lange).

Subsection *Tibiacystidinae* Smith & Sing. (1957). Cheilocystidia characteristically tibiiform (with a globose apical capitulum) or at apex less than 3 µm broad.

Type species: *G. tibiacystis* (Atk.) Kühner.

Stirps *Tibiicystis*. (Typically on *Sphagnum*; veil absent to rudimentary; spores mostly distinctly roughened, rarely subsMOOTH with distinct plage.)

*G. tibiicystis* (Atk.) Kühner; *G. subtibiicystis* Sing.; *G. luteolosperma* Smith & Sing.

Stirps *Triscopa*. (Typically not on *Sphagnum*; spores distinctly roughened, verrucose to marbled-punctulate; plage always distinct.)

*G. cascadensis* Sm. & Sing.; *G. uncialis* (Britz.) Kühner; *G. camerinoides* A.H. Smith; *G. pseudocerina* Sm. & Sing.; *G. tahquamenonensis* A.H. Smith; *G. hypsizyga* Sing. in Sm. & Sing.; *G. triscopa* (Fr.) Kühn.; *G. humicola* A.H. Smith; *G. laticeps* A.H. Smith; *G. subbadia* Sm. & Sing.; *G. pistillicystis* (Atk.) Sm. & Sing.; *G. aimara* Sm. & Sing.; *G. dominici* Sing.; *G. yungicola* Sm. & Sing.; *G. perrara* Sing. in Sing. & Corte; *G. marthae* Sing. (the 2 latter with cheilocystidia of the *tibiicystis*-type and the *Mycenopsis*-type often side by side, and therefore difficult to place); *G. mutabilis* A.H. Smith; *G. pteridicola* A.H. Smith; obviously also *G. fasciculata* Hongo.

Stirps *Sideroides*. (Spores entirely smooth to faintly marbled, with a slight plage-line or without it.)

*G. pseudocamerina* Sing. ex Sm. & Sing. (*G. josserandii* Kühner); *G. pseudostylifera* A.H. Smith; *G. perangusta* Smith & Sing.; *G. occidentalis* A.H. Smith; *G. columbiana* Sing.; *G. borealis* Sm. & Sing.; *G. cuspidata* A.H. Smith; *G. mammillata* (Murr.) Sm. & Sing.; *G. vinaceobrunnea* Sm. & Sing.; *G. sideroides* (Fr.) Kühner; *G. stylifera* (Atk.) Sm. & Sing.; *G. fuscobrunnea* A.H. Smith; *G. castaneocens* Sm. & Sing.; *G. agloea* Sm. & Sing.; *G. cephalotricha* Kühn.; *G. pallidispora* A.H. Smith; apparently also *G. cinctula* Orton; *G. larigna* Sing.; *G. luteofulva* Orton.

Subsection *Bulluliferae* Sm. & Sing. (1957). Cheilocystidia all vesiculose and pedicellate.

Type species: *G. bullulifera* Sing.

*G. bullulifera* Sing.; *G. coquimbensis* Sing.

Subsect. *Mycenopsidae* Sm. & Sing. (1957). Cheilocystidia variable but not as described for the *Tibiicystidinae* and *Bulluliferae*.

Type species: *G. mycenopsis* (Fr.) Kühner (sensu Kühner = *G. pumila*).

Stirps *Sphagnorum*. (Regularly associated with *Sphagnum*; veil present and often well developed; stipe generally exceptionally long; spores generally smooth to faintly ornamented, rarely finely verrucose.)

*G. paludosa* (Fr.) Kühn. (Galera, Kummer); *G. gibbosa* Favre; *G. semiglobata* Sing.; *G. sphagnorum* (Fr.) Kühn. [Galera hypnorum var. sphagnorum (Fr.) Quél.]; *G. taimbesinhoensis* Sing.; *G. andina* Sing.; *G. septentrionalis* A.H. Smith; *G. uchumachiensis* Sing. apud Sm. & Sing.

Stirps *Hypnorum*. (Not associated with *Sphagnum*, or only exceptionally near *Sphagnum*, at any rate not specifically sphagnicolous; spores distinctly verrucose to verrucose-rugulose under oil immersion even though the ornamentation may be

rather low, sometimes loosening with the perisporium but spores not calyptrate.)

*G. jaapii* Sm. & Sing. (*Pholiota mycenoides* (Fr.) Quél. sensu Jaap non Fr.; *Galerina*, Kühner; *Agaricus mycenoides* var. *applanatus* Lasch); *G. californica* Sm. & Sing.; *G. carbonicola* A.H. Smith; *G. decipiens* Sm. & Sing.; *G. rugisperma* A.H. Smith; *G. hypnorum* (Schrank ex Fr.) Kühn.; *G. alpestris* Sing.; *G. subhypnorum* (Atk.) Sing. (*Galerula*, Atk.; *Galerina hypnorum* sensu Smith & Sing. p.p. "American form"); *G. mniophila* (Lasch) Kühn.; *G. hypnicola* (Karst.) Sm. & Sing. (Galera, Karst.); *G. alluviana* Sm. & Sing.; *G. obscurata* A.H. Smith apud Sm. & Sing.; apparently also *G. glacialis* Sing.; *G. bryophila* (Murr.) Sm. & Sing.

Stirps *Pumila*. (Spores smooth to faintly marbled, otherwise all characters as in preceding stirps.)

*G. leucobryicola* Sm. & Sing.; *G. lacustris* A.H. Smith; *G. lubrica* A.H. Smith in Sm. & Sing.; *G. vexans* Sm. & Sing.; *G. rostrata* Sm. & Sing.; *G. naucoriooides* Sm. & Sing.; *G. allospora* Sm. & Sing.; *G. tundrae* Sm. & Sing.; *G. laeta* Sing. in Sm. & Sing.; *G. dicranorum* Sm. & Sing.; *G. fennica* Smith in Sm. & Sing.; *G. pumila* (Pers. ex Fr.) M. Lange; *G. luteosperma* Sm. & Sing.; *G. subfiliformis* Sing.; *G. polytrichorum* Sing. in Sm. & Sing.; *G. cainii* A.H. Smith in Sm. & Sing.; *G. emmetensis* Sm. & Sing.; *G. aberrans* Sm. & Sing.; *G. proxima* Sing. in Sm. & Sing.; *G. tattoooshiensis* A.H. Smith in Sm. & Sing.

Sect. 3. *POROSPORA* Sm. & Sing. (1957). Spores smooth or subsmooth with a small narrow germ pore but not truncate, often inamyloid. Pleurocystidia, none.

Type species: *G. stagnina* (Fr.) Kühner.

Stirps *Stagnina*. (Spores 10 µm and more long. Often sphagnicolous.)

*G. stagnina* (Fr.) Kühner (Galera, Kummer), with several varieties; *G. macrospora* (Velen.) Sing. (Galera, Velen.); *G. favrei* Sm. & Sing.; *G. nybergii* A.H. Smith in Sm. & Sing.; *G. subdecurrens* A.H. Smith.

Stirps *Lateritia*. [Spores smaller (less than 10 µm long). Lignicolous.]

*G. lateritia* (Murr.) Sing. (Naucoria, Murr.; *Galerula subannulata* Atk.); *G. camerina* (Fr.) Kühn. (sensu Fr., Favre, Moser non Kühn.); *G. pseudobadipes* Joss. ex Sm. & Sing.; *Agaricus inquilinus* Fr. sensu Secr. non al.); *G. subtruncata* Sm. & Sing. formerly inserted here, seems to be *Phaeomarasmius*.

Sect. 4. *INODERMA* Sm. & Sing. (1957). Pileus dry and innately fibrillose, or, if moist and hygrophanous, appearing distinctly innately fibrillose when faded, or with colored fibrils at least over the marginal zone of the pileus and than these also visible (more rarely not) on the basal portion of the stipe. Spores subsmooth but a line delimiting the plage area generally demonstrable in chloral hydrate mounts; hyphae of the outer layer of the epicutis with cystidiod terminal members or with crooked terminal members (these generally of a type similar to that of *Phaeomarasmius*); pleurocystidia present or absent. Mostly from the Pacific Coast area of North America.

Type species: *G. fibrillosa* A.H. Smith.

1. Acystidiate.

*G. tsugae* Smith & Sing.; *G. vaccinii* A.H. Smith; *G. fibrillosa* A.H. Smith.

2. With pleurocystidia.

*G. insignis* A.H. Smith.

**Note:** The cystidiate species may well be separated from the others in a special subsection.

Sect. 5. *PHYSOCYSTIS* Smith & Sing. (1957). Surface layer of pileus different from that of the preceding section - if fibrillose, the fibrils are whitish - and pleurocystidia present but different from those of the following section: if ampullaceous, they are broadly capitate-subcapitate and not with equal cylindric or tapering apex (neck), in their majority and also not bifurcate with finger-like appendages, otherwise broad and broadly rounded or with one short, broad, obtuse, apical mucro; cheilocystidia either like the pleurocystidia or of some other shape; spores ornamented, either as lowly and weakly as in the preceding section or more distinctly or even coarsely verrucose-ridged-rugose; basidia often 2-spored.

**Note:** In this section, several stirpes may be distinguished, much in the same way as in the following section, the epicuticular hyphae being variable from non-gelatinized and pigment-incrusted (in *G. pruinatipes* and others) to gelatinized (as in *G. cingulata*) and the spores vary from practically smooth but with semicircular plage-line (as in *G. pruinatipes*) to heavily ornamented (*G. cingulata* and others). The majority of species is South American and Western North American; only two species occurring in Europe.

**Type species:** *G. pruinatipes* A.H. Smith.

*G. microcephala* (Speg.) Sing.; *G. olympiana* A.H. Smith; *G. farinosipes* A.H. Smith; *G. pruinatipes* A.H. Smith (*Gymnopilus laricicola* Favre); *G. minor* Sing.; *G. subbulbilifera* Sing.; *G. cingulata* Sing.; *G. tetraspora* Sing.; *G. victoriae* Sing.; *G. velutipes* Sing., in Smith & Sing. (transitional to sect. *Naucoriopsis*); *G. viatica* Sing.; *G. papillata* Sing.; *G. arenaria* Sing.; *G. subpapillata* Sing.; *G. asteliae* Sing.; *G. peladae* Sing.; *G. elaeophylla* Sing.; *G. simocyboides* Sing.; obviously also *G. salicicola* Orton.

Sect. 6. *NAUCORIOPSIS* Kühn. (1935). Cheilocystidia and pleurocystidia present but the latter not broadly rounded as in section 5; epicutis not as in sect. 4; habit of the carpophores characteristically naucoroid (i.e. with initially incurved margin and profile of pileus not conic-campanulate when mature) or fleshy like *Pholiota* (because of a distinct annulus in many species); spores varying from nearly smooth but with the plage visibly delimited to heavily verrucose-ridged-rugose.

**Type species:** *G. marginata* (Fr.) Kühner.

Stirps *Autumnalis*. (Pileus with a distinct gelatinized epicutis - ixocutis - hence viscid to lubricous at first; annulus well developed or almost none.)

*G. subochracea* A.H. Smith; *G. viscosa* (Peck) Smith & Sing.; *G. autumnalis* (Peck) Smith & Sing.; *G. castaneipes* Smith & Sing.; *G. oregonensis* A.H. Smith apud Smith & Sing.; *G. megalocystis* Smith & Sing.; *G. cinnamomea* Smith & Sing.; *G.*

*discernibilis* Sing.; *G. dormientis* Sing.; *G. quinteroensis* Sing.; *G. phlegmacioides* Sing.

Stirps Marginata. (Epicutis generally not at all gelatinized or in few species very slightly and rather incompletely gelatinized, pileus merely moist - and sometimes fatty-shining - or mat when wet; annulus usually well developed.)

*G. infernalis* Sing.; *G. moelleri* Bas; *G. unicolor* (Fr.) Sing. (?*Agaricus xylophilus* Bull. ex St. Amans); *G. marginata* (Batsch ex Fr.) Kühner; *G. patagonica* Sing.; *G. physophora* Sing.; *G. helvoliceps* (Berk. & Curt.) Sing.; *G. vialis* A.H. Smith; *G. rudericola* A.H. Smith; *G. platyphylla* (Kauffm.) Smith & Sing.; *G. riparia* Sing.; *G. venenata* A.H. Smith; *G. sabuletorum* A.H. Smith.

Stirps Macquariensis. (Differing from stirps Autumnalis and Marginata in calyptrate spores.)

*G. macquariensis* Smith & Sing., obviously also *G. makereriensis* Pegler.

Stirps Cedretorum. (Differing from the preceding stirpes only in the absence of a persistent membranous annular veil - if a ring-like annular zone-band is present, it disappears at full maturity; differing from the following section in the more distinctly incurved margin of young specimens and/or the more naucoroid habit; differing from stirps Autumnalis in the absence of a well defined, distinct ixocutis on the pileus.)

*G. badipes* (Fr.) Kühn.; *G. mesites* Smith & Sing.; *G. cedretorum* (Maire) Sing.; *G. subglabripes* Smith & Sing.; *G. arenicola* A.H. Smith in Smith & Sing.; *G. subpectinata* (Murr.) Smith & Sing. (*Naucoria pectinata* (Berk. & Curt.) Sacc.); *G. hepaticicola* (Murr.) Smith & Sing.; *G. sulciceps* (Berk.) Sing.; *G. austroandina* (Sing. in Smith & Sing.) Sing. (*G. cedretorum* var. *austroandina* Sing.); *G. conspicua* Sing.; possibly *G. pinetorum* Métrod.

Sect. 7. *GALERINA*. Differing from the two preceding sections in typically mycenoid habit, i.e. margin of young specimens straight or pileus small and conic.

Type species: *G. vittaeformis* (Fr.) Sing.

Note: The separation of stirps Minima from sect. *Naucoroides* stirps Cedretorum, especially such species as *G. austroandina* in Patagonia is perhaps not possible on the strength of the mycenoid habit alone; it is possible that species with long, thin, cystidial neck should enter a stirps by themselves.

Stirps Minima. (Either veil present or dermatocystidia of the stipe confined to the apex, sometimes completely absent.)

*G. gamundiae* Sing. in Smith & Sing.; *G. inconspicua* Smith & Sing.; *G. reflexa* (Murr.) Smith & Sing.; *G. mollis* Smith & Sing.; *G. latispora* Smith & Sing.; *G. longinqua* Smith & Sing.; *G. rainierensis* Smith & Sing.; *G. saltensis* Sing.; *G. nordmaniana* Smith & Sing.; *G. funariae* Smith & Sing.; *G. thujina* Smith & Sing.; *G. mainsii* Smith & Sing.; *G. oreina* Smith & Sing.; *G. fontinalis* Smith & Sing.; *G. annulata* (Favre) Sing.; *G. subannulata* (Sing.) Smith & Sing.; apparently also *G. diabolissima* A.H. Smith and *G. nancyae* Smith in Smith & Sing.

*Stirps Vittaeformis.* (Veil none or extremely fugacious; dermatocystidia on the stipe descending towards base beyond the middle zone; dermatocystidia on the pileus present or absent.)

*G. umbrinipes* A.H. Smith; *G. atkinsoniana* A.H. Smith; *G. vittaeformis* (Fr.) Sing., with var. *vittaeformis*, var. *pachyspora* Sm. & Sing., var. *albescens* Sm. & Sing.; *G. violenta* (Berk.) Sm. & Sing.; *G. angustifolia* Sm. & Sing.; *G. karstenii* Sm. & Sing.; *G. pubescens* Sm. & Sing.; *G. perplexa* Sm. & Sing.

Sect. 8. *INOCYBOIDES* Sing. (1950). Pleurocystidia thick-walled and incrusted-muricate as in *Inocybe*; spores well ornamented, with distinct plage; veil present, at times strongly developed.

Type species: *G. nana* (Petri) Kühn.

*G. nana* (Petri) Kühn. (*Naucoria*, Petri; *Naucoria montana* Murr.; *Inocabe whitei* Velen.; *Galerula velenovskyi* Kühn.); obviously also *G. heimansii* W. Reijnders.

Sect. 9. *PSEUDOTUBARIA* Sm. & Sing. (1957). Spores quite smooth and without a germ pore, callus, plage, or any vestiges of an exosporial ornamentation. Pleurocystidia and cheilocystidia present.

Type species: *G. fuegiana* Sing.

*G. clavus* Romagnesi (*Naucoria*, Kühn. & Romagnesi); *G. fuegiana* Sing.; *G. pal-lida* (Pilát) Horak & Moser (*Velomycena*, Pilát).

## GENERA OF UNCERTAIN POSITION

*Quercella* Velen., *Ceské Houby*, p. 495, 1921. "Small fungi, with the habit of *Galera*; pileus strongly viscid, hygrophanous, with transparent lamellae; stipe thin, fibrillose, watery-fleshy, without belt and without cortina; lamellae free, rather thick, the old ones pale ferruginous; spores almond-shaped, smooth". - In a jar, containing alcohol-formalin and labeled so as to indicate it among other specimens (*Psathyra alnetorum*, *Limacium cinereum*, *Telamonia tremulina*), the type material of *Quercella aurantiaca* Velen. is preserved and was kindly put at my disposal by Dr. Z. Urban, Prague. After eliminating the other specimens, the type specimen was studied by me. It is the specimen which corresponds to the original diagnosis. This has the following characters: Spores  $8.5-11.3 \times 5.2-6.8 \mu\text{m}$  rugose or warty, not smooth, without germ pore and plage, rusty ochraceous brown, ellipsoid; basidia 4-spored, ventricose,  $27-35 \times (7)-8-8.5 \mu\text{m}$ ; cystidia (cheilocystidia?) fusoid-ampullaceous with subcapitate ( $\times 3-4 \mu\text{m}$ ) tip,  $2-2.5 \mu\text{m}$  across below tip,  $4-5 \mu\text{m}$  broad in lower portion, about  $26 \mu\text{m}$  long, not thick-walled, not numerous; trama hyphae filamentous,  $3-5 \mu\text{m}$  broad, yellow, clamp connections present. Taking these characters together, *Conocybe* and *Pholiota* are excluded from consideration so that *Quercella* can only be a cortinariaceous genus. The viscid, hygrophanous pileus excludes *Alnicola*, *Gymnopilus*, and *Dermocybe*. Absence of a plage and the presence of clamp connections excludes *Galerina*. Spore pigmentation and ornamentation exclude the pale-spored Cortinariaceae. Consequently, *Quercella* could be *He-*

*beloma*, *Cortinarius*, or *Phaeocollybia*. The shape of the cystidia and the glutinous pileus appear to indicate *Phaeocollybia*; the habit, particularly the absence of a pseudorrhiza or georrhiza, and the *Cortinarius*-like odor seem to indicate some *Cortinarius*. The spores are somewhat more voluminous than in the known European *Phaeocollybiae*. The cystidia are uncommon but not impossible for *Cortinarius*. The colors and odor do not suggest any known species of *Hebeloma*. Finally, *Quercella* may theoretically be a thus far unknown genus independent of the above-mentioned, although this appears to be rather improbable.

Consequently, I believe that *Quercella* is a synonym of *Cortinarius*, but cannot offer any definite proof. One would have to assume that Velenovsky's claim regarding the absence of a cortina is based on incorrect observation.

*Locellina* Gillet, *Champignons*, p. 428, 1876. "Ochrosporous. A volva tearing at the top, with persistent base, bulbiform; annulus arachnoid; spores brownish". Gillet. The type species is *L. alexandri* Gillet from France. It is viscid on the pileus, with a rusty dusted cortina, and white stipe, the base somewhat bulbous, and the volva is drawn very conspicuously almost as in *Amanita*. If a slight exaggeration is taken for granted, and if the spores are not smooth as they are shown on Gillet's plate, this might well be a *Cortinarius*. This is what Quélet thinks (*Enchiridion*, p. 78, 1886) who identifies it with *Cortinarius delibutus*. Fayod considers it as one of the genera of his tribus *Cortinariés* which consists of various elements of the genus now recognized as *Cortinarius*. In the author's opinion, it is theoretically impossible to prove that *Locellina* is nothing but *Cortinarius*, but Gillet's picture strongly suggests that genus, and there is scarcely a chance that Gillet's genus belongs anywhere else. Under no circumstances should extra-European species be described in or transferred to *Locellina* since they are likely to be something entirely different (e. gr. *L. californica* Earle).

*Cyphellopus* Fayod, *Ann. Sc. Nat., Bot.* VII. 9: 365. 1889 [*Acetabularia* (Berk.) Sacc., *Syll.* 5: 6. 1887, non Lamour.; *Agaricus* subgen. *Acetabularia*, Berk., *Linn. Soc. Journ.* 18: 389. 1881]. "Velum universaliter a pileo discretum; hymenophorum discretum; lamellae liberae; sporae pallide fulvae v. brunneae". Berkeley. This diagnosis is emended and translated by Massee, *British Fungus Flora* 2: 232. 1893 as follows: "Pileus regular; gills free from the stem; stem central; universal veil present, remaining as a volva at the base of the stem; spores tawny or brown". The type species is *Agaricus acetabulosus* Sowerby ex Berk., Sowerby pl. 303. As for the plate, some may be inclined to see in it a *Pluteus*, some a *Coprinus*. Berkeley said that the original specimen was (1881) still attached to the original plate. In this case it should be an easy task for any modern taxonomist to tell where this species belongs. Sowerby makes the following comment on his species: "Found near Millbank, Westminster [England] ... This is very like a poor specimen of *Agaricus congregatus* [*Coprinus micaceus*] but the pileus is more plaited. The lamellae are remarkably glandular on their sides; and instead of a bare base it stands in a little socket-like volva". Massee (l.c., p. 233) says: "The present species has not been noted since Sowerby's time, and is a very uncertain production. Judging from the magnified section of the gills [in Sow. pl. 303], the glands on their sides are cysti-

dia". Saccardo recognized Berkeley's subgenus as a genus but later put it in synonymy with *Locellina* Gillet. The same procedure is also followed by Cooke. This is undoubtedly a mistake. Already W.G. Smith, Massee, and Fayod pointed out that *Locellina* is not generically identical with *Acetabularia*. Yet, *Acetabularia* is a homonym of an older algal genus. Therefore, Fayod's proposal of a new name for *Acetabularia* (Berk.) Sacc. is nomenclaturally correct and acceptable. Fayod has not seen the species himself but thinks, evidently judging from what is known from publications in the English literature, that *Cyphellopus* (= *Acetabularia*) is comparable to *Volvariella* and close to his own section *Celluloderma* of *Pluteus*. But it may be a volvate *Coprinus*. For more guesses as to its identity, see Pearson, *Trans. Brit. Mycol. Soc.* 20: 54-55. 1935. (Annotations by Quélet, René Maire, and Rea) and Watling, *British Fungus Flora* 3: 43-44. 1982.

Whatever the final result - *Cyphellopus* has no chance of being a valid genus under the present arrangement.

*Weinzettlia* Vel., *České Houby* 3: 514. 1921. "Fleshy fungus with the appearance of *Cortinarius cinnabarinus*; pileus convex, innately scaly; stipe cylindrical ... brittle-fleshy, fibrillose outside, canaliculate-hollow from the start ...; lamellae distant, thick; stipe in the young stage connected with the pileus by a fibrillose cortina; spores ovoid, smooth, yellow; cystidia on the edge and on the sides of the lamellae, pillar-shaped, rounded; spore print rusty." Velenovsky. The type species is *W. rubescens* Vel. from Czechoslovakia, with red viscid pileus and white, red-fibrillose stipe, flesh and lamellae reddening on injury; spores 8-10 µm long; growing on black humus. Type specimens were kindly provided by Dr. Z. Urban and Dr. Svrček and studied by me. In one jar material from Třeboň is conserved together with what seems to be *Pholiota sulphurea* (the former with hollow, the latter with solid stipe). I am not certain whether this is identical with the second collection from Přelouč which agrees well with the diagnosis. The Přelouč material has smooth ellipsoid spores (6)-6.5-7.7 µm long, yellow, but they are obviously scarce and immature. If the Třeboň specimen is identical the mature spores would be 5.5-8.8-(10) × 4.3-5.5 µm, verrucose, ferruginous, without germ pore and plage; only occasionally one finds - in the Přelouč-type - a spore with a slight ornamentation. Pleurocystidia are definitely absent and cheilocystidia doubtful; clamp connections are present (but many septa without a clamp). Macroscopically, this fungus is remarkable because it is now somewhat purple (in acetic-acid-formaline mixture), has strictly hollow stipe which, however, has been cut just above the base. Obviously, the Třeboň material is the holotype.\*

I am inclined to think that both the Třeboň and the Přelouč material are identical with each other, or at least congeneric, and that both are identical with a species related to or similar to *Cortinarius bolaris* as has also been suggested by Dr. Svrček.

Nevertheless, it should be kept in mind that no absolute proof is offered for this disposal of the genus *Weinzettlia*.

\*An effort to obtain topotype material from Třeboň was unsuccessful; according to Dr. Kubička, Wein-zettl collected in many places even rather far from Třeboň, and all this material was labeled "Třeboň" by Velenovský.

## CREPIDOTACEAE (Imai) Sing.

Type genus: *Crepidotus* (Fr.) Quél.

Syn.: *Crepidoteae* Imai, Journ. Fac. Agr. Hokk. Imp. Univ. 43: 238. 1938.

**Characters:** Spore print brownish to light yellow, rarely subfuliginous spores without a germ pore and an exosporial ornamentation in the form of warts without a true plage, with a weakly to well developed differentiation of endo- and episporium, not angular in any view, rarely lemon-shaped in frontal view; if ornamented, the ornamentation is due to spines which cause the spores to appear punctate or verruculose when focussed upon their surface but most frequently with ornamentation type XI when seen in optical section (rarely type XII), habit omphalioid to collybioid, or pleurotoid, or cyphelloid; hyphae with or without clamp connections; the usual reagents without much action, not causing color reactions with the carpophores; hymenophoral trama not distinctly bilateral, and if there are conductive elements, these are also not arranged in a bilateral manner; trama of the pileus at times partly gelatinized, inamyloid; veil thin membranous to cortinoid, or absent; lamellae not repeatedly forked, sometimes absent; cheilocystidia in lamellate forms present, but pleurocystidia rarely observed\*, spores uni- or binucleate, inamyloid. On various débris, wood, humus, soil, sand, deep moss, etc.

**Limits:** The Crepidotaceae are in a way intermediate between the Cortinariaceae and the Entolomataceae, and they are also close to the Paxillaceae. The genera with ornamented spores (ornamentation of type XI, sometimes XII, rarely XI-II) differ from the respective genera of the Cortinariaceae in the structure of the spore wall - a difference also showing in EM sections where the immersed and sometimes confluent columns appear as free, very narrow and quite isolated cones (hollow) giving the impression of a type VI ornamentation whereas the cortinariaceous genera typically appear rugose-verrucose with the ornamentation irregular and consisting of broad warts which show irregular cavities. Since, in addition, every single genus of Cortinariaceae is easily separable from the genera of Crepidotaceae, it results that there is no difficulty in delimiting the two families. On the other hand, the Crepidotaceae have been compared with the Tricholomataceae, the Entolomataceae, and the Paxillaceae.

There is now no more need to point out that *Pleurotellus* is by no means related or congeneric with *Omphalina*-like genera (like *Leptoglossum*) or *Clitopilus*-like genera. Nevertheless, it should be mentioned that very often the small, white, pale-spored pleurotoid agarics are distinguishable from each other, even generically, only by careful microscopical analysis. I do not know to what degree this reflects affinity, but the reader should be cautioned that it is fairly easy - if one does not dispose of a spore print - to confuse a certain number of *Crepidotus* and *Pleurotellus* species (Crepidotaceae) with certain groups of *Marasmiellus* and other small Tricholomataceae and/or with pleurotoid species of *Clitopilus*, *Rhodocybe*, and *Entoloma*. This is the reason why it is impossible to interpret such "Pleuroti" as

\*Only in some species of *Crepidotus* (cystidioles or metuloids) and *Melanomphalia* (cystidia or metuloids) have pleurocystidia been observed.

*Agaricus septicus* or *A. dictyorrhizus*. This situation has found its expression in the position of the Crepidotaceae in the present classification viz. between Cortinariaceae and Entolomataceae.

As for the Paxillaceae, a greater reactivity of the carpophores and their pigments with  $\text{FeSO}_4$ , KOH,  $\text{NH}_4\text{OH}$ , formol, metol, a generally more strongly developed bilaterality of the hymenophoral trama and, among species with echinate spores, absence of ornamentation type XI (as seen in light microscopy) in all species and individual spores is characteristic for that family as compared with the Crepidotaceae. In contrast to a large number of ectotrophically mycorrhizal species in both Cortinariaceae and Paxillaceae, there are no ectomycorrhizal species in the family Crepidotaceae. The Paxillaceae are obviously closer to the Boletaceae than to the Crepidotaceae as shown by chemotaxonomy.

Both Crepidotaceae and Paxillaceae have the hilum of the spores of the open-pore type whereas in both Tricholomataceae (excepting Lyophylleae and Terminomycteae) and Entolomataceae, a hilum of the nodulose type is indicated by Pegler & Young (1971).

#### KEY TO THE GENERA

- A. Agaricoid genera with well developed lamellae.
- B. Habit clitocyboid, collybioid, or omphalioid, i.e. stipe central.
  - C. Chemical reactions strong; spores globose or subglobose with ornamentation not of type XI, or absent, or no cheilocystidia differentiated (cf. fam. Paxillaceae).
    - C. Chemical color reactions generally weak; spores rarely subglobose and then neither smooth nor with ornamentations of type VI, V etc.; cheilocystidia generally present and well differentiated, if poorly differentiated - spore ornamentation strictly of type XI (light microscopy).
      - D. Epicutis - a cutis; spore wall smooth or ornamentation type XII, homogeneous, weakly pigmented, often tending to collapse in 5% KOH mounts; lamellae mostly adnate to decurrent.
        - 181. *Tubaria*, p. 680
      - D. Either the epicutis is not a cutis or the spore wall is not homogeneous.
        - E. Spore wall homogeneous, smooth, not particularly pale colored; epicutis - an often fragmentary subhymeniform layer consisting of often dermatocystidioid or sphaerocyst-like terminal members erect to somewhat obliquely ascendant, parallel with each other or fasciculately bunched together.
          - 183. *Simocybe*, p. 685
        - E. Spore wall heterogeneous, ornamentation of type XI, poorly to strongly pigmented; epicutis variable.
          - 182. *Melanomphalia*, p. 683
  - B. Habit pleurotoid.
    - F. Stipe either absent, or in form of a pseudostipe, or else sublateral, or simply eccentric, in the latter case - clamp connections absent or spores not smooth and not with homogeneous wall; epicutis not as in *Simocybe* (cf. above under letter "E"), or if so - clamp connections absent or spores not smooth and not with homogeneous wall.
      - G. Spore print deeper than "cork" if the spores have homogeneous wall; clamp connections present or absent.
        - 184. *Crepidotus*, p. 687
      - G. Spore print "cork" (M & P) or "cram buff" to "chamois" (Ridgway); spores absolutely smooth with homogeneous wall; clamp connections absent.
        - 185. *Pleurotellus*, p. 692
    - F. Stipe eccentric, usually well developed in mature specimens (even if relatively short, curved or oblique); clamp connections present; spores smooth and with homogeneous wall; epicutis as in *Simocybe* (see "E" above).
  - A. Cyphelloid genera without lamellae, with smooth hymenial surface, small (reduced series).
    - H. Spores ornamented; clamp connections present or absent.

- I. Spores oblong, pale melleous; sterile surface with cystidioïd hairs which are distinctly elongate; clamp connections none. 188. *Pellidiscus*, p. 696
- I. Spores ellipsoid; sterile surface with irregular cystidioïd short elements; clamp connections present. 189. *Chromocyphella*, p. 697
- H. Spores with homogeneous wall, smooth; clamp connections present.
- J. Outermost layer of sterile cup surface formed by a trichodermial palisade consisting of well delimited incrusted or non-incrusted, often more or less thick-walled hairs; cups accompanied by or rising from a conspicuous brown stroma consisting of bunches of brown subparallel hairs. 187. *Phaeosolenia*, p. 695
- J. Outermost hyphal layer of cups forming a loose trichodermium of hyphal hairs which are incrusted.
- K. Spores well colored shortly before reaching maturity, with a wall about  $0.4 \mu\text{m}$  thick, ellipsoid with somewhat flattened inner side, a hyaline endosporeum distinguishable in mature spores; hairs filamentous, with equal rounded-obtuse tip; on bark, perhaps always associated with Sphaeriales; cystidia none; stroma sparse. 186. *Episphaeria*, p. 694
- K. Spores at first hyaline or subhyaline, eventually becoming pale stramineous to brown in most species; wall thinner than  $0.4 \mu\text{m}$ , and endosporeum difficult to distinguish in the light microscope; shape of spores and of hairs variable from species to species; cystidia sometimes present; stroma sometimes well developed, tomentose.

See *Cyphelopsis* and *Merismodes*, p. 848

## 181. TUBARIA (W.G. Smith) Gillet

*Champignons*, p. 537. 1876; em.

*Type species*: *T. furfuracea* (Pers. ex Fr.) Gillet.

*Syn.*: *Agaricus* subgenus *Tubaria* W.G. Smith, *Clavis Agar.*, p. 21. 1870.

*Characters*: Habit omphalioid to collybioid, pileus mostly distinctly hygrophanous, non-viscid, with a cuticle consisting of repent, thin-walled hyphal elements, some of them in some species slightly incrusted by an intercellular or epicellular pigment, some of the hyphae with guttulate contents in some species, without any dermatocystidia or spherocysts, and not forming a trichodermium or palisade; lamellae adnexed to decurrent, rather narrow to more often broad; hymenophoral trama regular to subregular; spores with non-ornamented wall which is indistinctly double or simple, rarely with an ornamentation of type XII, the smooth spores easily collapsing after reaching maturity (and the wall often crumpled-rough for that reason), reniform to almond-shaped, or ellipsoid to almost boat-shaped or subcylindric, without germ pore or callus, without plage, rather small (but more than  $5 \mu\text{m}$  long) to medium sized (somewhat above  $10 \mu\text{m}$ ), brownish (ochraceous, ochraceous-cinnamon, light ferruginous-ochraceous, etc.) in various (not very deep) shades, e. gr. between "desert" and "centennial br.", or "Gold leaf", "Antique gold", "Mosul" (Maerz & Paul) when observed in print; basidia normal but sometimes 2-spored; cystidia none on the sides of the lamellae but the edge of the lamellae always heteromorphous or nearly heteromorphous from the cheilocystidia which are of varying shape and size according to the species, and often even in a single preparation but always conspicuous, rarely with finger-like appendages; stipe central and as long or more often longer than the diameter of the pileus, with or without veil, more frequently with a thin membranous, white or whitish veil that only very rarely leaves an annular belt, without pseudorrhiza; hyphae of the context with

clamp connections. On various dead vegetable matter, fallen fruits, leaves, needles, on wood, deep moss, and on the soil or sand.

*Development of the carpophores:* Hemiangiocarpous in *T. furfuracea* according to Walker, and probably hemiangiocarpous in all species of *Tubaria*; monovelangiocarpous, stipitocarpic (Reijnders).

*Area:* Probably cosmopolitan.

*Limits:* This genus differs from all other genera of the Crepidotaceae by the characters of the spores, combined with the characters of the carpophore (central stipe) and seems to be closest to *Crepidotus*. As for spore ornamentation see Cléménçon (1977).

*Tubaria* is separated from *Galerina* by several important characters, in the first place by the characters of the spores which have thinner walls with a simpler structure, no plage and no verruculose exosporial ornamentation; the subgenus *Tubariopsis* of *Galerina*, without plage, differs in having clampless septa; the sect. *Pseudotubaria* differs in stronger spore wall and the presence of pleurocystidia. The genera *Phaeomarasmius* and *Simocybe* differ in the structure of the epicutis (among other characters of equal weight). Their spores may appear somewhat similar under the microscope because they are also somewhat thin-walled in some species of *Simocybe* and *Phaeomarasmius* but the differentiation of the endosporium is usually better discernible in these genera than in *Tubaria*. Two species of *Phaeomarasmius* have been inserted in *Tubaria* by several authors, mainly by Kühner, viz. *Naucoria carpophila* and *N. ferruginosa*, but the first of these two has since been transferred to *Floccularia* (= *Phaeomarasmius*) by Kühner & Romagnesi. These species have a very different structure of the covering layer of pileus and stipe, and are actually close to other species of *Phaeomarasmius*, not to *Tubaria*.

Harmaja (*Karstenia* 18: 55-56, 1978) has taken up Kühner's (1975) opinion that *P. confragosa* belongs in *Tubaria*. I do not consider Harmaja's conclusion correct since it is based on the comparison of some anatomical characters of subgenus *Phaeomarasmius* only, not of *Phaeomarasmius* as a whole as accepted in this book (see also p. 392). The differences in epicutis structure and spore print color between *P. confragosa* and *Tubaria furfuracea* are correctly described but omission is made of the fact that in the former the hyphae of the epicutis are characterized by incrusting pigment whereas the outermost layer of the covering of the pileus of *T. furfuracea* is pigment-less. This observation, by the way, was also made by Kühner whose proposition of congenitivity of this pair of species is extended more conditionally and hesitantly to other species of *Phaeomarasmius*. Having studied and restudied over 30 species of *Phaeomarasmius* and innumerable collections of various *Tubarias* I can still see no reason whatever to separate *Phaeomarasmius* subgen. *Phaeomarasmius* from the rest of the species, and even less evidence in favor of joining some or all of them with *Tubaria*.\* This position is confirmed by the fact that "N."

\*To recognize *Flammulaster* but single out, at the same time, one species, *P. confragosus*, for transfer to *Tubaria*, as proposed by Orton (*Notes R. Bot. Gard. Edinburgh* 41: 619, 1984), is possible only if the fact that *Phaeomarasmius* is not based on one microscopic character and is a homogeneous natural genus which absorbs *P. confragosus* with ease is totally misunderstood. On the other hand the incorporation of that species in *Tubaria*, indeed, appears to be cumbersome and erroneous.

*granulosa* (*Phaeomarasmius!*) is bivelangiocarpous (Reijnders) whereas the true Tubarias are monovelangiocarpous.

Kühner & Romagnesi subordinate *Tubaria* as a subgenus to an all-embracing genus *Naucoria* (containing aside from *Phaeomarasmius* and *Simocybe* also *Alnicola* and *Tubaria*, and a group of *Phaeomarasmius* which these authors call *Floccularia*), a solution we find as convenient for the nomenclaturist as we consider it unacceptable from a taxonomic point of view, even if *Tubaria* were considered as belonging to the Cortinariaceae or Strophariaceae rather than to the Crepidotaceae. Our own reason for putting *Tubaria* with *Crepidotus* in a separate family is the existence of a mostly extra-European group, the genus *Melanomphalia*, which is apparently close to *Crepidotus* since it has spores extremely similar to those of *Crepidotus* sect. *Echinospori*, from which it differs mainly in the central stipe.

Those who still feel with Fries that *Tubaria* is indeed related to other families rather than to the rest of the Crepidotaceae are of course free to remove it from the latter family, but where? In the Strophariaceae it would place itself near *Pachylepyrium* and *Kuhneromyces*, both clearly unrelated. In the Cortinariaceae, only *Galerina* is comparable.

It may be argued that some species of *Tubaria* e.gr. *T. furfuracea* have binucleate spores much like *Galerina*, and that *Tubaria* should therefore be transferred to the Cortinariaceae. Aside from the fact that in the latter family *Tubaria* has no relatives, it seems to me that this cytological character alone cannot be of great weight as long as not several species of all crepidotaceous genera have been studied in this regard.

A few species of *Tubaria* in the wider sense (as it was originally interpreted by Gillet and Saccardo) have nothing in common with either *Tubaria* in the restricted sense, or with the Cortinariaceae as delimited by us. They belong in *Psilocybe* (Strophariaceae), and differ from other similar genera in the Crepidotaceae and Cortinariaceae in deeper colored spore print, a broad truncate germ pore, and thick spore walls.

*State of knowledge:* Romagnesi was the first author who has paid attention to the taxonomy of this genus. He treated only the European species, and his keys and descriptions do not seem applicable to American material. We are now admitting in *Tubaria* a total of 15 species but it may be expected that more species exist inasmuch as the Tubarias of Asia, Africa, and Australia are still practically unknown.

*Practical importance:* Unknown.

## SPECIES

*T. dispersa* (Pers.) Sing. (Agaricus, Pers. non Fr.; *Tubaria autochthona* (Berk. & Br.) Sacc.); *T. minutalis* Romagnesi; *T. pallidispora* Lange; *T. jaffuelii* (Speg.) Sing. (Naucoria, Speg.); *T. conspersa* (Pers. ex Fr.) Fayod (sensu Romagnesi); *T. trigonophylla* (Lasch) Fayod (sensu Cooke); *T. furfuracea* (Pers. ex Fr.) Gillet [including several microspecies or varieties such as (now sometimes distinguished as

species) *T. pellucida* (Bull. ex Fr.) Gillet sensu Romagnesi; *T. gregoriana* (Speg.) Sacc.; *T. anthracophila* Karst.; *T. subcrenulata* Murr.; *T. fuscifolia* Murr., *T. pseudopartites* Sing.; *T. pentstemonis* Sing.; *T. strophosa* Sing.].

## 182. MELANOMPHALIA Christiansen

*Friesia* 1: 288. 1936.

*Type species: M. nigrescens* Christiansen.

*Syn.: Horakomyces* Raithelhuber, *Metrodiana*, Sonderheft 8: 17. 1983.

*Characters:* Hbit of a small *Gomphidius* or *Paxillus*, omphaloid or even mycenoid to collybioid, not pleurotoid, with at first incurved margin, or with straight margin, generally rather thin-fleshy to moderately fleshy; lamellae at first ascendant or not, narrowly adnexed to more frequently adnate to decurrent; stipe central, with basal mycelium; veil present or absent, scarcely ever annuliform; volva absent; spores small to large (between 4.5 and 14  $\mu\text{m}$  long) with a faintly heterogeneous to strongly heterogeneous episporium (ornamentation type XI, light microscope) and often also a perisporial ornamentation, short ellipsoid to fusoid, without a true "plage", with or without an apical discontinuity but never with a strongly truncate germ pore, inamyloid. Cheilocystidia present, but sometimes scattered and basidiomorphous, more frequently dense and numerous, and of different shapes, clavate, fusoid, ampullaceous, ventricose-constricted, even capitate; pleurocystidia more frequently absent than present, but at times very prominent and even metuloid in one species. Clamp connections present. Epicutis an ixocutis, a cutis, or with bunched together dermatocystidioid terminal members of a trichodermium or else with ascendant terminal members of a cutis, more rarely with a hymeniform epicutis consisting of broad erect elements and these sometimes with inflating wall. Hymenophoral trama regular. Spore print varying from pale ochraceous to ochraceous-brown to olive fuliginous (for example "Mosul", "Yucatan", "ginger" of Maerz & Paul but also much paler and much darker). On the ground, on earth and on debris, but also frequently on dead woody matter, trunks, culms, or among mosses, in and outside the forest.

*Development of the carpophores* and nuclear cytology not studied.

*Area:* Widely distributed in both North and South America, Europe (there probably adventitious), tropical East Africa, New Guinea; the largest number of species known from temperate and tropical South and Central America.

*Limits:* The spore wall of the Crepidotaceae, especially of *Melanomphalia*, often gives the impression of punctate spores when these are seen not in optical section and not with a good immersion lens. Under these circumstances, they can easily be confused with spores of cortinariaceous genera such as *Cortinarius*, *Phaeocollybia*, or *Galerina*. The fruit bodies of these three genera often appear very similar macroscopically, so that they might be and have been confused. How can *Melanomphalia* be separated from similar cortinariaceous genera? The species of *Melanomphalia*

are not ectotrophically mycorrhizal as are those of *Cortinarius*. This circumstance makes it possible to realize in the field that some collections, otherwise much like *Cortinarius*, *Inocybe*, or *Alnicola*, are actually none of these. Moreover, they could not be *Tubaria* or *Simocybe* which they also resemble because of the heterogeneous episporium of their spores. A number of species of *Melanomphalia* are even constantly lignicolous, or grow in typical anectrotrophic stands of trees. Furthermore, the range of colors of spore prints in the genus, although often individually comparable with those of *Cortinarius*, is much wider. This is exemplified by *M. nigrescens* (where the spores are olive-fuliginous) and *M. omphaliopsis* (where they are milk-coffee colored - "Mosul" M & P). Finally, those species of *Melanomphalia* that for any other reason come close to *Cortinarius* in their appearance possess cheilocystidia quite different from those observed in some *Cortinarii*. No species of *Melanomphalia* has any affinity with any true *Cortinarius* (although it is possible that some undescribed species of *Melanomphalia* might have been incorrectly referred to *Cortinarius*).

If *Melanomphalia* is compared with *Galerina*, it should be noted that the spores are quite different: All species of *Melanomphalia* are devoid of a well delimited strictly suprahilar plage, but have hyphae with clamp connections whereas those species of *Galerina* without a plage have no clamp connections. Under the EM the spore sections show an irregularly fractured or discontinued layer of dense material on the outside (just inside the "perisprium") with irregular cavities in *Galerina* whereas in *Melanomphalia* the punctuation is in reality due to narrow, erect cone-like spinules with a straight internal cavity elongated in a direction corresponding to the (divergent) direction of the cones (as in *Crepidotus*), but may occasionally fuse with neighboring cones to form short crests. Very rarely, in *Melanomphalia vernifera* for example, I have observed areas with homogeneous wall surface which may or may not be located suprahilarly but are certainly not restricted to that area; these non-ornamented regions of the spore wall are not marked by a semicircular ragged line of ornamentation material and cannot be compared with or homologized to the plage of *Galerina*. A similar situation has been observed in other genera of the Crepidotaceae with ornamented spores e. gr. *Crepidotus* and *Chromocyphella*.

Aside from the difference in spore ornamentation, *Gymnopilus* differs also by more brightly ferruginous spore print color. *Phaeocollybia* which under the light microscope might sometimes show ornate similar to those observed in *Melanomphalia*, has a pseudorrhiza or georrhiza never seen in *Melanomphalia*.

The other crepidotaceous genera have either spores with homogeneous wall or else they are strictly pleurotoid or cyphelloid.

In the Paxillaceae there are only three genera with ornamented spores. These spores are, however, different in ornamentation and/or shape and the pigments are different; the respective genera - *Phyllobolites*, *Neopaxillus* and *Ripartites* are thus quite different from *Melanomphalia* even where the slight bilaterality of the hymenophoral trama is indistinct or overlooked.

*State of knowledge:* 23 species are now known to me.

*Practical importance:* Unknown.

## SPECIES

*M. viscosa* Sing.; *M. vernifera* Sing.; *M. cortinariooides* Sing.; *M. pacifica* Sing.; *M. inocybooides* Sing.; *M. columbiana* Sing.; *M. emarginata* Sing.; *M. omphaliopsis* (Sing.) Sing.; *M. smithii* Sing. ad int.; *M. alpina* (A.H. Smith) Sing.; *M. platensis* (Speg.) Sing.; *M. thermophila* (Sing.) Sing.; *M. platyphylla* Sing.; *M. nigrescens* Christiansen; *M. crocea* (Speg.) Sing.; *M. mazatecorum* Sing.; *M. hymenocephala* Sing.; *M. baeospora* Sing.; *M. universitaria* Sing.; *M. dwyeri* Sing.; *M. argipoda* Sing.; *M. pellucida* (Murr.) Sing. (*Naucoria pellucida* Murr., *Mycologia* 4: 78. 1912; *Galerina*, Smith & Sing.); *M. leucocephala* Sing. ined.; obviously also *Tubaria verruculosa* Pegler and *Phaeocollybia tentaculata* Horak.

### 183. SIMOCYBE Karst.

*Bidr. Finl. Natur Folk* 32: xxii, 1879.

*Type species: Simocybe centunculus* (Fr.) Karst.

*Syn.: Ramicola* Velen., *Mykologia* 6: 76. 1929.

**Characters:** Carpophores small, mycenoid or collybioid or pleurotoid (but with distinct stipe), thin-fleshy to membranous with rather thin stipe; pileus more or less hygrophanous (but the epicuticular elements sometimes covering up the hygrophanous layer beneath), hemispheric to conic-campanulate, later repand and often applanate, with straight to somewhat incurved margin in youth; epicutis in more or less discontinuous patches of dermatocystidia and cystidioid terminal hyphal cells intermixed or not with spherocysts, and these elements forming hymeniform or sub-hymeniform structures whereby they may be bundled together in fascicles; lamellae adnexed to adnexed-subfree, more rarely sinuate, but frequently broadly adnexed, sinuate-adnexed or broadly adnate; spore print ochraceous to somewhat olivaceous or brownish, e. gr. 15-J-12, "butterscotch", between "Seminole" and "wigwam", "raw umber", "buffalo", "golden corn" (M & P); spores under the microscope brownish, ochraceous, ochraceous melleous, but never subhyaline, smooth and with homogeneous wall, without germ pore but sometimes with a slight discontinuity (thinning of the wall layers, or a weak callus) at the apex, ellipsoid, ovoid, subfusoid, obovoid to somewhat wedge-shaped, often with applanate to concave inner side and then appearing bean-shaped or reniform in lateral view (profile), with moderately thick but firm (not collapsing easily in 5% KOH) wall which is distinctly to indistinctly double (epi- and endosporium), rarely over 9, never more than 11  $\mu\text{m}$  long, i.e. small to medium sized; basidia normal but sometimes 2-spored; cheilocystidia always present and distinct, usually making the edge of the lamellae (which may be discolored) heteromorphous; pleurocystidia none; hymenophoral trama regular; hyphae with clamp connections; stipe usually thin, with conspicuous or inconspicuous basal mycelium; veil scarcely developed and very fugacious, practically absent in most species; pseudorrhiza absent. On wood, sawdust, leaves and other plant débris and not ectomycorrhizal.

*Development of the carpophores:* Paravelangiocarpous and marginal veil very ephemeral consisting of some hyphae which connect the pileus with the stipe in the primordium in the type species (Reijnders).

*Area:* From the temperate zones of both hemispheres to the tropics.

*Limits:* This genus can rather easily be distinguished from the other crepidotaceous genera. It differs from *Phaeomarasmius* in the characters of the epicuticular layer and the type of development of the carpophores.

Romagnesi has combined this genus with *Agrocybe* (1962). Although Romagnesi is to be commended for diligently and laboriously exploring and enumerating all the arguments in favor of acceptance of a gradual transition between *Agrocybe* and *Simocybe*, our reasons for rejecting such an affinity have already been stated by Singer & Moser (1965) and have been further corroborated by my type studies (G) of *S. laevigata* (Favre) Orton, the species which was particularly mentioned by Romagnesi as being intermediate between *Agrocybe* and *Simocybe*. It is undoubtedly a species closely related to other species of *Simocybe* and corresponding to that genus on the basis of all characters stressed in the generic description. The epicutis of all *Agrocybes* is different from that of all *Simocybes*; in addition the spores of *Agrocybe* generally have a truncate germ pore and where this is wanting, pleurocystidia are present.

Orton (1960) has combined *Simocybe* with *Alnicola*. Not only is there an exosporial ornamentation of the Cortinariaceae-type present in all species of *Alnicola*, but there is also a sharp biological and phytogeographical separation line between these two genera; consequently, Orton (1969) changed his mind and accepted separate genera.

*State of knowledge:* The genus is not, as some authors think, a small split group from *Naucoria* sensu lato (see also p. 848) but a rather large genus containing now 38 species. The neotropical species have been monographed by the present author (1973, 1977).

*Practical importance:* Unknown.

## SPECIES

*S. tiliophila* (Peck) Sing.; *S. rubi* (Berk.) Sing. (*Naucoria effugiens* Quél.; *Crepidotus haustellaris* (Fr.) Kummer sensu Pilát Kühner & Romagnesi vix Fr.); *S. reducta* (Fr.) Karst.; *S. junquillea* Sing.; *S. tucumana* Sing.; *S. curvipes* (Sing.) Sing.; *S. amazonica* Sing.; *S. corticalis* Sing.; *S. magna* Sing.; *S. fulvifibrillosa* (Murr.) Sing.; *S. ovalis* Sing.; *S. amara* (Murr.) Sing.; *S. puberula* (Peck) Sing.;\* *S. bruchii* (Speg.) Sing.;\*\* *S. reductoaffinis* Sing.; *S. unicolor* (Peck) Sing.; *S. ser-*

\*c.n. (= *Crepidotus puberulus* Peck, *Bull. Torr. Cl.* 25: 324. 1898).

\*\*c.n. (= *Crepidotus bruchii* Speg., *Bol. Acad. Nac. Cienc. Córdoba* 29: 128, "as "Bruchi").

*ratula* (Murr.) Sing.; *S. aestivalis* Sing.; *S. laevigata* (Favre) Orton; *S. tepeitensis* (Murr.) Sing.; *S. alachuana* (Murr.) Sing.; *S. semiglobata* (Murr.) Sing.; *S. atomacea* (Murr.) Sing.; *S. praeandina* (Sing.) Sing.; *S. pallidissima* (Sing.) Sing.; *S. polytropa* (Sing.) Sing.; *S. polytropoides* Sing.; *S. subvelutina* (Sing.) Sing.; *S. subolivacea* (Murr.) Sing.; *S. olivaceiceps* (Sing.) Sing.; *S. citrinipes* (Murr.) Sing.; *S. melleiceps* (Murr.) Sing.; *S. microlepis* Sing.; *S. coroicensis* Sing.; *S. urosphaera* Sing.; *S. pantelaeodes* (Sing.) Sing.; *S. olivaceonana* (Sing.) Sing.; *S. sumptuosa* (Orton) Sing.; *S. centunculus* (Fr.) Karst. with var. *obscura* (Romagnesi) and "forme alpine" (Singer 1950) both of which may be independent, closely related species. Apparently also *Naucoria decolorata* Malençon ex Galán, Ortega & Moreno (Pleuroflammula, Bon & Moreno). According to Horak also the following species: from New Zealand and New Guinea: *S. phlebophora* Horak; *S. unica* Horak; *S. pruinata* Horak; *S. luteomellea* Horak; *S. tabacina* Horak; *S. austrorubi* Horak (and, of somewhat doubtful position: *S. fuscoconica* Horak; *S. argillacea* Horak; *S. mutabilis* Corner & Horak; *S. subfulva* (Cleland) Horak). According to Pegler et al. (1980) also *S. antarctica* Pegler in Pegler, Spooner & Lewis Smith.

#### 184. CREPIDOTUS Kummer

*Führ. Pilzk.*, p. 21, 1871.

*Type species: C. mollis* (Schaeff. ex Fr.) Kummer.

*Syn.: Agaricus tribus Crepidotus* Fr. *Syst. Mycol.* 1: 272. 1821.

*Crepidotus* (Fr.) Quél., *Champ. Jura Vosg.*, p. 138. 1872-3

*Dochmiopus* Pat., *Hymen. Fur.*, p. 113. 1887.

*Derminus* Schröter in Cohn, *Krypt.-Fl. Schlesien, Pilze* 1: 578. 1889.\*

*Tremellopsis* Pat. apud. Duss, *Fl. Crypt. Ant. Fr.*, p. 223. 1904.

*Tremellastrum* Clem., *Gen. Fung.*, p. 105. 1909.

?*Phialocybe* Karst., *Bidr. Finl. Nat. Folk* 32. xxii. 1879.

**Characters:** Habit pleurotoid (Pl. 47,2); pileus with an indefinite cuticle, or if the cuticle is well differentiated as a cutis or trichodermium, the latter consists of repent or ascendant to erect, thin, filamentous hyphae which sometimes are forked, rarely with very scattered and inconstant dermatocystidioid bodies, rarely these so short-clavate and dense that the epicutis appears almost elliptical, the colored species having the walls of the superficial hyphae pigment-incrusted, some species yellow, pink, or red but more species are between rusty or brown and white, more often closer to the latter, i.e. hyphae all devoid of pigment; underneath the cuticle or the surface layer, in many species, a narrower to broader layer of strongly gelatinized hyphae (Pl. 3); lamellae variously attached to the base, or concurrent, rounded or attenuate, often decurrent if a stipe is present, not connected by anastomoses, narrow or broad; hymenophoral trama regular to subregular, consisting of interwoven to subparallel hyphae, at times all of them running in different directions and - though they are all elongate to filiform - rather versiform in a single

\*If Staude's "genera" (but cf. *Mycologia* 47: 270-2. 1955) were recognized as such *Derminus* (Fr.) Staude would be a synonym of *Pholiota* (nom. cons.).

preparation but always the majority strictly axillary arranged, usually pigment-less but in a few species slightly pigmented, in one species with crystalline vinaceous pigment, the hyphae varying in density, from loosely arranged to rather densely packed; spore print about "clay color" (Ridgway), in some species more yellowish than "clay color" (reaching "honey yellow" in others more cinnamon, viz. between "oak wood" and "Terrapin" (Maerz & Paul), or Pl. 13, K-10 "chipmunk", "Englisch oak", "raw sienna", "kis kilim" to "cocoa", "tiffin", "olive wood", "clove", "Madrid", 13 K 10/11, "Peruvian br." (so from the beginning by dry dehydration), between "cattail" and 15-H-12) but never as deep fuscous or rusty as in the Strophariaceae (*Melanotus* and *Pleuroflammula*), melleous to brownish melleous, often rather pale and with a rusty tinge (from the imbedded ornamentations) under the microscope, with rather thin an simple wall, but in some species with an indistinct endosporium, the outer stratum of the wall often perforated with imbedded very short cylindric spines or more rarely warts or ridges which are usually but not always somewhat deeper colored than the space between them, under oil immersion the outer stratum of the spore wall appearing perforated (ornamentation type XI) and when focused on the spore surface - punctate, more rarely warty or ridged, or else spores entirely smooth and non-ornamented, from nearly perfectly globose (but with oblique hilar appendage) to rather oblong in certain species (but then never smooth), often ellipsoid or short-ellipsoid, and at times with mucronate apex, without a germ pore, only rarely with an indistinct one, but occasionally with an indistinct callus; basidia normal but sometimes bisporous; cystidia none on the sides of the lamellae but cystidioles often present on the sides of the lamellae; cheilocystidia always present (even though they may be only terminal members of the filamentous hyphae of the hymenophoral trama (often gelatinized then); the latter are not always crowded enough to make the edge heteromorphous but usually rather numerous, varying in size and shape according to the species and often rather versiform in a single preparation, sometimes metuloid; stipe rarely well developed and then comparatively short and more or less eccentric (and then spores ornamented), sometimes rudimentary, visible only from below (hymenophoral surface), not from above, or else well developed in the primordia and then gradually obliterated; veil none, or very indistinct; context consisting of hyphae, with or without clamp connections. On wood, and herbaceous stems, rarely on the earth or attached to mosses, or on fallen parts of ferns, palms, etc. occasionally parasitic on living trees. Chemical reactions with the ordinary reagents rather weak.

*Development of the carpophores:* Unknown.

*Area:* Cosmopolitan.

*Limits:* This genus can be separated from all genera of the Crepidotaceae according to the characters indicated in the key. The genus most closely related to it, is *Pleurotellus* which can be distinguished by several correlated characters (see there).

In other families, there are certain species which have been confused with the *Crepidoti* but actually are not very closely related though, at times, they may look somewhat similar. These are *Pleuroflammula*, *Melanotus*, and *Pyrrhoglossum*. The latter has more richly colored, warty spores and darkens with alkalis; *Pleuroflam-*

*mula* and *Melanotus* have a different type of spores, especially the latter genus where the spores are strikingly truncate from a well developed germ pore.

Some authors consider *Paxillus panuoides* as a *Crepidotus*, but the differences between that species and all the other *Crepidoti* are so striking, and the similarities between it and the other *Paxilli* so numerous, it can hardly be expected to be retained in *Crepidotus* in a modern classification.

**State of knowledge:** A North American monograph by Hesler & Smith (1965) and a neotropical one by the present author (1972) as well as numerous type studies by Singer, Pilát, Hesler & Smith, and Horak make *Crepidotus*, after many years of neglect, one of the better known genera of the Agaricales. For the European mycologist Pilát's monograph (1948) and Orton's key (1960) will still be a useful source of information although some corrections and emendations by Singer (1947, 1973) and Hesler & Smith (1965) should be taken into consideration. There are now 106 species of *Crepidotus* sufficiently known to be inserted in the enumeration of the species below.

An interesting and valuable contribution by Pegler & Young (*Kew Bull.* 27: 311-323, 1972) appeared which contains a revised key to the British species of the genus *Crepidotus*; it is illustrated by 17 photographs representing *Crepidotus* spores under the scanning microscope. While it may be true that "there is no evidence" (as the authors state) of any interruption of the episporium, perforations in the exosprium, or of a persistent perisporial layer, I cannot agree that the ornamented spores of *Crepidotus* appear very similar to those observed in cortinariaceous species. Here again, a correct interpretation of the ultrastructural surface morphology of the spores is possible only if both surface markings as seen in the scanning microscope and sections of the spore wall are known. Such sections were prepared by Dr. Cléménçon in collaboration with the present author, and these convinced us that the spinules of *Crepidotus* spores are of a quite different type as compared with the ornate spores of *Cortinarius*-spores (and those of other Cortinariaceae). The perisprium does not show as a continuous layer since obviously it is deteriorated and/or depressed between the spinules but its traces appear visible in Pegler & Young's photos (e. gr. Pl. 27, Fig. 1, Pl. 28, Fig. 1). The material between the spinules (interpreted by me and others as episporial layer, but apparently wrongly so) is obviously liquid or semiliquid, or at any rate not showing in EM photographs. Whether this is a consequence of fixation methods or an indication of free spinules (in an air space) cannot be decided at present, nor can I decide whether the perisprium visible under the best optical conditions under oil immersion in light microscopy, becomes fragmented or obliterated because of imbedding methods.\* However, even so, Pegler & Young's contribution is very valuable since the photos

\*Cléménçon (1977), on the basis of careful EM studies on the spore wall of *C. cesatii*, *C. sphaerosporus*, and *C. subsphaerosporus*, has arrived at the conclusion that it must be assumed that the spines are free in an air space and that the ornamentation type seen in the light microscope is, at least in the species studied by him, an optical illusion. In *C. appplanatus* Cléménçon observed an ornamentation of tree-trunk-like spines connected by an incomplete root-like reticulation, and a viscous outer layer, the mocostratum, covers all "trunks" and the surface between them.

show the differences between the two main sections of *Crepidotus* (*Echinospori* and *Crepidotus*) and well definable differences in spore ornamentation of the various species of the former.

According to Horak (*Arctic and Alpine Mycology* p. 107. 1982) *Simocybe antarctica* Pegler in Pegler et al. "belongs to a yet undescribed genus" and seems to have "very close affinities to two other moss-inhabiting South American taxa, viz. *Crepidotus velutoaffinis* [*C. velutinoaffinis* Sing. apud Dennis is apparently meant] and *Neopaxillus bryogenus* Horak". Not only is the spore ornamentation of *S. antarctica* non-existent according to Pegler, or at any rate quite different from that of the other species mentioned, but the epicutis is described as precisely that of a true *Simocybe*, whereas the other species cited by Horak seem to have different structures. As described and illustrated, *Neopaxillus bryogenus*, not known to me, is hardly anything but a species of *Galerina*, as already suspected by Horak (1979).

Horak (1977) has also described a lignicolous species as *Phialocybe improvisa* Horak (*Austr. Journ. Bot. Suppl. Ser.* 10: 33. 1983) which differs from other species of sect. *Echinospori* in "cuticula pilei ex hyphis clavatis epithelium efformantibus" but the species, unknown to me, is so summarily described (clamp connections?) that its position remains somewhat doubtful. However, other species fully described by him as *Crepidotus* species, with metuloids, are highly interesting inasmuch as they appear to be restricted to the Southern Hemisphere (New Zealand, New Caledonia, South Africa, but with one collection quoted from Java); yet there are transitional forms (*C. parietalis* Horak, with thin-walled cheilocystidia but these covered with crystalline or amorphous incrustations). Since the lamellae and spores, when mature, appear to be well pigmented, a possible confusion with *Hohenbuehelia* can easily be corrected, and these species obviously belong in *Crepidotus* sect. *Echinospori* and, since they are clamp-bearing, in subsection *Porporophorini*. These, for *Crepidotus*, new characters, viz. metuloid cheilocystidia and epithelium-like epicutis, are not entirely surprising in the Crepidotaceae since similar structures have already been observed and described in *Melanomphalia*.

With regard to the intrageneric taxonomy of *Crepidotus*, the reader is referred to my recent monograph (*Nova Hedwigia*, Beih. 44. 1973).

**Practical importance:** Some *Crepidoti* are rather harmless wood destroyers (e. gr. *C. paxilloides* on oak ties). Other species are edible.

One species, *C. citricolor*, causes a rot in shaded branches of *Citrus*.

## SPECIES

**Sect. 1. ECHINOSPORI** Pilát (1929). Spores with heterogeneous or spinulose wall (in the sense that they are punctate when focussed upon the upper surface of the spore because of small, thin columns, rarely narrow sheets of contrasting material, appearing immersed in a hyaline subperisporial layer in the light microscope, but appearing as free, narrow cones which rarely are fused on their sides and are hollow when seen in EM sections, these ornamentations often projecting beyond the outline

of the spore which then appears to be finely echinulate, rarely verrucose to almost cristate, but also often with the circumference appearing quite smooth (in the light microscope); spore shape from spherical to elongated.

Type species: *C. carpaticus* Pilát.

Subsection *Porpophorini* Sing. (1947). Hyphae and base of basidia clamped.

Type species: *C. applanatus* (Pers. ex Fr.) Kummer.

*C. roseus* Sing.; *C. roseolus* Sing.; *C. citrinus* Petch; *C. polylepidis* Sing.; *C. nyssicola* (Murr.) Sing.; *C. cristulatus* Sing.; *C. velutinoaffinis* Sing.; *C. latifolius* Peck with var. *latifolius*, var. *praelatifolius* (Murr.) Sing., var. *appendiculatus* Sing. and var. *veraecrucis* Sing.; *C. quitensis* Pat.; *C. harperi* Sing.; *C. decipiens* Sing.; *C. crocophyllus* (Berk.) Sacc.; *C. fuvifibrillosus* Murr.; *C. aquosus* Murr.; *C. cuneiformis* Pat.; *C. truncatus* Petch; *C. confertus* Hesl. & Sm., *C. epicrocinus* (Berk. & Br.) Sacc.; *C. nephrodes* (Berk. & Curt.) Sacc. (*C. malachius* (Berk. & Curt.) Sacc.); *C. putrigenus* (Berk. & Curt.) Sacc.; *C. hygrophanus* Murr. (if not too close to the preceding or following species); *C. applanatus* (Pers. ex Fr.) Kummer with var. *applanatus* and var. *subglobiger* Sing.; *C. cystidiosus* Hesler & Smith; *C. subapplanatus* Hesler & Smith; *C. subaureifolius* Hesl. & Smith; *C. episphaeria* (Berk.) Sacc. ("episphaerius"; *C. pagonatus* (Kalchbr.) Sacc.); *C. icterinus* Sing.; *C. subcroceitinctus* Hesler & Smith; *C. croceitinctus* Peck; *C. brunswickianus* (Speg.) Sacc.; *C. xanthocephalus* Sing.; *C. rubriceps* Sing.; *C. septicoides* (Sing.) Sing.; *C. longicystis* (Hesler & Smith) Sing.; *C. amygdalosporus* Kühn., in Kühn. & Romagnesi (?*C. trullisporus* Pegler); *S. submollis* Murr.; *C. carpaticus* Pilát; *C. cesatii* (Rab.) Sacc.; *C. sphaerosporus* (Pat.) Lange; *C. eucalypti* (Torrend) Sing.; *C. leptomorphus* (Berk.) Sacc.; *C. bullulifer* Sing.; *C. subsphaerosporus* (Lange) Kühn. & Romagnesi; *C. wakefieldiae* Pilát; *C. subverrucisporus* Pilát; *C. echinosporus* Henn.; *C. montanensis* Hesler & Smith; *C. martini* Sing.; *C. inhonestus* Karst.; *C. lundellii* Pilát (if not too close to preceding); *C. subtilis* Orton; *C. kauffmanii* Hesler & Smith; *C. mexicanus* Sing.; *C. guzmanii* Sing.; *C. palmarum* Sing. in Sing. & Digilio; *C. australis* Sing.; *C. luridus* Sing. with var. *luridus*, var. *oaxacae* Sing., and var. *minutus* Sing.; *C. catamarcae* Sing.; *C. paxilloides* Sing.; *C. macedonicus* Pilát; *C. luteolus* (Lambotte) Sacc.; *C. pezizula* (Berk. & Br.) Sacc.; *C. stercorarius* Sing.; *C. reniformis* Velen. (*C. epibryus* (Fr.) Quél. sensu Pilát vix Fr.); *C. eburneus* Hesler & Smith; *C. vulgaris* Hesler & Smith; *C. confertus* Hesler & Smith; *C. variabilis* (Pers. ex Fr.) Kummer.; also *C. parietalis* Horak; *C. hirsutellus* Horak; *C. aureus* Horak; *C. nanicus* Horak (the three latter species apparently related to the likewise metuloid-bearing *C. episphaeria* (Berk.) Sacc.; also *C. pilosiceps* Sing. ined.).

Subsect. *Aporpini* Sing. (1947). Hyphae and base of basidia without clamps.

Type species: *C. cinnabarinus* Peck.

*C. cinnabarinus* Peck; *C. citricolor* Sing.; *C. defibulatus* Sing.; *C. unicus* Hesler & Smith; *C. versutus* (Peck) Sacc.; *C. igapoensis* Sing. ined.; apparently also *C. effusus* Pegler.

Sect. 2. *CREPIDOTUS*. Spore wall completely homogeneous, without any kind of ornamentation.

Type species: *C. mollis* (Schaeff. ex Fr.) Kummer.

Subsection *Fibulatini* Sing. (1947). Hyphae with clamp connections.

Type species: *C. albidus* Ell. & Ev.

*C. albidus* Ell. & Ev. with var. *albidus*, var. *boliviae* and var. *bisporus* Sing.; *C. acanthosyrinus* Sing.; *C. albissimus* Murr.; *C. serotinus* Sing.; *C. podocarpi* Sing. & Digilio; *C. parlatorei* Sing. in Sing. & Digilio; *C. antillarum* (Pat. apud Duss) Sing. (*Tremellopsis*, Pat. apud Duss; *C. cinchonensis* Murr.); *C. betulae* Murr.; *C. caspari* Velen. (*C. autochthonus* Lange); *C. fragilis* Joss. (if not too close to the preceding species).

Subsection *Crepidotus* (*Defibulatini* Sing. 1947). Hyphae and base of basidia without clamps.

Type species: *C. mollis* (Schaeff. ex Fr.) Kummer.

*C. tuxtlae* Sing.; *C. molliformis* Sing.; *C. levisporus* Sing.; *C. yungicola* Sing.; *C. sublevisporus* Sing.; *C. citri* Pat.; *C. subaffinis* Pilát; *C. parasiticus* Mass. ex Pilát; *C. calolepidoides* Murr.; *C. fraxinicola* Murr.; *C. mollis* (Schaeff. ex Fr.) Kummer; *C. alveolus* (Lasch) Kummer (if sufficiently different from the preceding); *C. xanthophaeus* Sing.; *C. brasiliensis* Rick; *C. uber* (Berk. & Curt.) Sacc.; *C. melleus* (Berk. & Br.) Petch (*Aschersonia*, Berk. & Br.); *C. ampullicystis* Sing.; *C. epigloeus* Sing.; *C. eucalypticola* Sing.; *C. variisporus* Sing.; *C. calolepis* (Fr.) Karst. with var. *heterocystis* Sing.; spp. *tigrensis* (Speg.) Sing. (with var. *januarius* Sing. and var. *aristoteliae* Sing.); ssp. *polycystis* Sing.; apparently also *C. spathulata* Bres. - Apparently also *C. geophilus* (Murr.) Redhead (*C. pubescens* Bres.)

## 185. PLEUROTELLUS Fayod

*Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 339. 1889.

Type species: *Pleurotus hypnophilus* (Berk.) Sacc.\*

Syn.: *Calathinus* Quél., *Enchiridion* p. 46, 1886 non Rafinesque (1836).\*\*

\*On the type species see Singer, *Persoonia* 2: 143. 1961. Horak (1968) prefers as type species the binomial *Pleurotellus graminicola* Fayod which amounts to the same.

\*\*Donk and, following him, Horak (1968) state erroneously that the type species of *Phyllotus* is *A. porrigens*, and that the same species is also the type of *Calathinus*. As far as *Calathinus* is concerned, this is an academic question since *Calathinus* is a homonym. However, I disagree with these authors on the principles which guided them in their decision, on the presentation of their case and on the disregard for the rules of the Code as its precise wording stands rather than as it might or should be. It is an inadmissible argument that the scope and approximate covering of a Friesian section being similar to that of *Calathinus* and *Phyllotus* should cause them to have obligatorily the same type species which also "must" occur in the Friesian section. It is equally incorrect to state that Earle "chose" or "designated" a type since he merely indicated a type following the rules he recognized; these rules do not provide for the selection of a lectotype. The Code prescribes that the "first selection" of a lectotype must be followed; if Earle's is not a selection but an indication based on mechanical method of selection (Art. 8.1), the first

**Characters:** Much like *Crepidotus* but combining a filamentous cutis on the sterile surface with clamp-less hyphal septa ("simple" septa) and an extraordinarily pale spore print color ("cream buff" to "chamois" Ridgway or slightly more pinkish e. gr. "cork" Maerz & Paul); spores under the microscope subhyaline to pale brownish yellow, thin-walled, smooth, with homogeneous wall, cyanophilic, inamyloid, not appearing angular in any position, without a germ pore or callus; cystidia on the sides of the lamellae absent. On wood and herbaceous trash, cortex, roots, occasionally of living, mostly dead Cormophyta.

**Development of the carpophores:** Gymnocalypous (Watling).

**Area:** All over the temperate zone of both hemispheres, more uncommon in the tropical belt.

**Limits:** The macroscopical appearance of the species of *Pleurotellus* - small scarcely pigmented pleurotoid carpophores without a distinct stipe or an extremely fugacious one, can be found in the genera *Crepidotus*, *Pleurotus*, *Clitopilus*, *Entoloma*, *Nothopanus*, *Marasmiellus*, and *Marasmius*. While all these genera are anatomically quite different from *Pleurotellus*, their position is mostly difficult to establish unless one disposes of a good spore print. It is for that reason that I have refrained from interpreting such classical species as *Agaricus septicus*, *A. dictorhizus*, as long as no type material is available.

The hiatus between *Crepidotus* and *Pleurotellus* is not stronger than it is generally between genera of the Crepidotaceae. It may well be questioned as Hesler & Smith do, whether "*Pleurotellus* as a genus distinct from *Crepidotus* will stand the test of close scrutiny", but this questioning cannot be based on our present knowledge of the two genera. We cannot delimit genera by anticipation of future discoveries. After the publication of three modern monographs, the two genera are still perfectly well distinguishable unless a much wider generic concept is permitted, one that does not agree with the generic concept adopted in this book. Any crepidotaceous species combining the habit of *Crepidotus* with homogeneous spore wall, pale spore print color, and absence of clamp connections belongs in *Pleurotellus*, not *Crepidotus*.

Some authors still include in *Pleurotellus* such pigmented species as *P. acerosus* whose affinities are not with *Crepidotus* but with *Omphalina* and *Leptoglossum* (Tricholomataceae). The presence of an intraparietal pigment and white spore print makes it easy to exclude such species from *Pleurotellus* and the Crepidotaceae. Furthermore, white-spored species with the general characters of *Resupinatus* should likewise be excluded. They differ among other characters in the presence of clamp connections.

selection must be followed. Lengthy discussions as to which type species should have been selected by those who actually selected a type are sterile exercises and may even - inadvertently - lead to an obstruction of all efforts to come to a common language in mycology. These remarks should not be construed as being directed against the detailed and meritorious efforts of some authors, including Donk, to assemble all facts leading to a correct selection of a lectotype or the correct indication of a type, but they should be taken as a warning what wherever important decisions are concerned, all data should be checked and weighed instead of accepted as coming from an authority.

With regard to the type species, I quote Orton (1960, p. 665) "Although I have no personal knowledge of it, I prefer ... to accept Pilát's interpretation of *P. hypnophilus* rather than Singer's". Mycologists who have personal knowledge of this species would perhaps like to know how these supposedly opposed interpretations differ. Horak and I have studied the type of *P. graminicola* and agree that it is *P. hypnophilus* sensu Fayod. According to Hesler & Smith (1965, p. 22, 36) *C. herbarum* (*P. hypnophilus*?) differs from "*C. pubescens* Bres." (what they mean is our *P. hypnophilus*), in pip-shaped, sublanceolate to somewhat ellipsoid to subovoid (versus subfusoid or pip-shaped, slightly allantoid in profile) spores and clavate, cylindric or ventricose (versus filamentous ... the basal portion sometimes clavate-enlarged) cheilocystidia. I found in *C. herbarum* spores larger than given by Hesler & Smith, cylindric to ellipsoid-oblong, on one side applanate, and could not find good cheilocystidia. *C. pubescens* Bres. is a completely different species belonging to *Crepidotus*.

*State of knowledge:* Only two species are known.

*Practical importance:* *P. chioneus* occurs as a weed fungus in beds of the Cultivated Mushroom (*Agaricus bisporus*) on the casing, but hardly causes any appreciable damage.

## SPECIES

*P. hypnophilus* (Pers. ex Berk.) Fayod [Pleurotus, Sacc.; Crepidotus herbarum (Peck) Sacc.\*]; Pleurotellus, Sing.; Claudopus commixtus Bres.; Pleurotellus graminicola Fayod]; *P. chioneus* (Pers. ex Fr.) Kühn. (sensu Pilát 1935, p.p., non 1950) (Pleurotus, Gillet; ?Agaricus arenarius Lasch non Lév.); perhaps also *Agaricus cretatus* Berk. & Br.\*\*

### Reduced series: 186. EPISPHAERIA Donk apud Sing. ex Donk

*Persoonia* 2: 336. 1962.

*Type species:* *Cyphella fraxinicola* Berk. & Br.

*Characters:* Habit pezizoid, cup-shaped, minute, sessile, pubescent-tomentose and white outside, ochraceous-brownish on the smooth hymenial surface; hymenium consisting of clavate (3-)4-spored basidia without siderophilous granulation; cystidia, none; trama in the type species not gelatinized, of only one kind of hyphae, these filamentous, mostly hyaline, running almost subparallel with each other; covering layer of the sterile outside of the cups consisting of a loose but not gelatinized layer of hyphal hairs which are hyaline, or have a brownish intraparietal pig-

\*See preceding page under "Limits".

\*\*A specimen of Fungi Brit. Exs. no. 502, 1877 (FH) has spores about  $10.5 \times 4.5 \mu\text{m}$ , not angular in polar view; no clamps found.

ment, incrusted by apparently inorganic colorless granules up to the rounded-obtuse tip, filamentous; all hyphae inamyloid, with numerous clamp connections (in the type); spores with a smooth homogeneous wall about  $0.4 \mu$  thick, consisting of a poorly individualized colored episporium and a hyaline endosporium with or without a minute discontinuity at the apex, but neither with a typical truncate germ pore nor a distinct callus, ellipsoid, ovoid, or reniform, ochraceous brownish when mature, medium sized, inamyloid. On bark, perhaps always on Sphaeriales.

*Development of the carpophores:* Unknown.

*Area:* Until now found only in Europe, but there are apparently also representatives from extra-European areas, according to Donk (oral communication).

*Limits:* *Episphaeria* differs from all other cyphelloid agaricoid genera in the smooth, colored spores and the pilose-hyphous tomentum consisting of partly pigmented incrusted elements. It is obviously related to the *Crepidoti* of sect. *Crepidotus*, especially the non-gelatinized species of stirps *Antillarum* from which it differs in the absence of lamellae and the small and pezizoid fruiting.

*State of knowledge:* Only one species is known to this author.

*Practical importance:* Unknown.

## SPECIES

*E. fraxinicola* (Berk. & Br.) Sing. ex Donk (Cyphella, Berk. & Br.; Phaeocyphella, Rea.).

Reduced series: 187. **PHAEOSOLENIA** Speg.

*An. Mus. Nac. Bs. As.* 8: 53. 1902.

*Type species:* *P. platensis* Speg.

*Characters:* Habit cyphelloid or densely aggregate ("Solenia" type) and always associated with a colored stroma consisting of long brown hairs, external sterile surface of cups covered with a trichodermial palisade of brown (fewer hyaline) hairs which are (fewer not) incrusted by crystals which make the outline of the hairs appear diverticulate, and where strongly incrusted, the cups appear macroscopically white especially in youth and in the upper regions of the cup, otherwise cup brown, with brownish smooth hymenial surface which points away from the substratum unless the cup is high and bent over in the stroma; hymenium consisting of basidia which are rather short and normally 4-spored; cystidia none, excepting at the rim of the cups where some cystidioid hairs may occur; trama of cups consisting of hyaline subparallel, thin-walled, filamentous hyphae with clamp connections, with inamyloid walls, not gelatinized, running from the base towards the rim of the cup; spores smooth although often with small internal corpuscles, subhyaline when immature, brown (ochraceous-melleous brownish) when mature, lemon-shaped to

ellipsoid, often laterally compressed like spores of *Psilocybe* section *Psilocybe*, small to medium sized, without germ pore but at times with a slight callus, with homogeneous wall which consists of a thin epi- and a thin endosporium, episporium smooth. On wood and other plant tissue.

*Development of the carpophores:* Unknown.

*Area:* Southern Europe, Southern Asia, Southern South America and probably all over the warm-temperate, subtropical and tropical-montane regions.

*Limits:* This genus differs from all other cyphelloid, agaricoid brown spored genera in the palisadic arrangement of the well delimited hair zone on the outside of the cups and also in the structure of the stroma. The stroma is virtually always present but it is not equally developed in all collections. An Argentine collection of *P. platensis* showing very conspicuous islands of stroma while other collections from the same region show only sparse stromatic formations in restricted portions of the population, is not, on any other grounds, separable from the type form.

*State of knowledge:* The author knows only three species, closely related to each other.

*Practical importance:* Unknown.

## SPECIES

*P. platensis* Speg.; *P. endophila* (Cesati in Rab.) Donk apud Sing. ex Donk; *P. inconspicua* (Berk. & Curt.) Donk apud Sing. ex Donk; apparently also *P. pelargonii* (Kalchbr. apud Thümen) W.B. Cooke and *P. densa* (Berk.) W.B. Cooke.

### Reduced series: 188. **PELLIDISCUS** Donk

*Persoonia* 1: 89. 1959.

*Type species:* *Cyphella pallida* Berk. & Br.

*Characters:* Habit cyphelloid, resupinately attached, sessile, pileus, discoid, pezizoid, small, inside of disc fertile, with a smooth hymenial surface consisting of basidia; outside sterile, pilose from hyphal hairs which are partly free, near margin often cystidioid; basidia short and broad, of the kind typical of many species of *Crepidotus*, cystidia in hymenium absent; marginal cystidioid hairs thin-walled, hyaline, not incrusted, inamyloid, smooth; spores as in sect. *Echinosporeae* of *Crepidotus*, melleous, punctate, elongate, without germ pore and without plage, medium sized; clamp connections absent. On wood.

*Development of the carpophores:* Unknown.

*Area:* Europe, perhaps holarctic.

*Limits:* The spore color and ornamentation differentiate this genus from all other

cypelloid reduced genera of Agaricales known until now. It differs from the other genera of the Crepidotaceae in the habit and smooth hymenial surface (absence of a differentiated hymenophore) and the characters indicated in the key to the genera, particularly from the following genus (*Chromocyphella*) in paler spores which have a thinner wall, no germ pore and non-peeling wall layers, also in the not or scarcely pigment-incrusted hyphae which have no clamp connections.

*State of knowledge:* Only one species is known, but this has been studied and described completely by Donk and was re-examined by this author.

*Practical importance:* Unknown.

## SPECIES

*P. pallidus* (Berk. & Br.) Donk (Cyphella, Berk. & Br.; Cyphella bloxamii Berk. & Phill. apud Berk. & Br.).

### Reduced series 189. CHROMOCYPHELLA de Toni & Levi

*Naturalist* 1888: 158. 1888.

*Type species:* *Cymbella crouanii* Pat. & Doassan apud Pat.

*Syn.:* *Cymbella* Pat. apud Doassan & Pat., *Rev. Mycol.* 8: 27. 1886, non Agardh (1830).

*Phaeocarpus* Pat., *Hymen. Europ.*, p. 154. 1887, non Mart. & Zucc. (1824).

*Phaeocyphella* Pat., *Bull. Soc. Mycol. Fr.* 9: 135. 1893 (nom. nud.); *Ess. taxon.*, p. 57. 1900.

*Phaeocyphella* Speg., *An. Mus. Nac. Hist. Nat. Bs. As.* 19: 278. 1909.

*Characters:* Habit cypelloid; pileus stipitate, with a short attenuated base or sessile, cup-shaped (pezizoid) to discoid, small, inside of disc fertile, without hymenophore, hymenium consisting of basidia, hymenial cystidia none; sterile outside silky to pubescent, with a covering of short, often curved or branched hyphae with thin walls; spores as seen under the light microscope, oil immersion, much like those of *Setchellilogaster* (Secotiaceae), with ornamentation of type XI, not or slightly and narrowly truncate at apex, but with a germ pore, outer layer of spore wall often cracked and leaving smooth plage-like areas either near the hilar appendage or elsewhere, well pigmented (ochraceous brown in KOH), short ellipsoid to subglobose, medium sized, wall about 0.6 µm thick; clamp connections present; hyphae incrusted by pigment. Among and on mosses over wood.

*Development of the carpophores:* Unknown.

*Area:* Temperate region of the northern hemisphere reaching the montane zone of Southern Asia (Java), also in the southern hemisphere (Argentina).

*Limits:* This is the only reduced genus with spores as described above. It has a spore ornamentation as sometimes found in *Crepidotus* (sect. *Echinosporeae*), and the germ pore is not essentially different from that of some species of *Crepidotus* sect. *Crepidotus*. A true plage, such as found in *Galerina* is not present. Color and shape

of the spores, presence of clamp connections and an incrusting pigment (such as also found in the upper layers of the cuticle of some *Crepidot*) distinguish this genus from the preceding one.

**State of knowledge:** Two species are well known.

**Practical importance:** Unknown.

## SPECIES

*C. muscicola* (Fr.) Donk (Cyphella, Fr.; Cymbella crouanii Pat. & Doassan apud Pat.; Phaeocarpus, Pat.; Cyphella, Sacc.); *C. sphaerospora* (Speg.) Sing. (Phaeocyphella, Speg.).

## ENTOLOMATACEAE Kotlaba & Pouzar

*Ceská Mykologie* 26: 218. 1972.

**Type genus:** *Entoloma* "(Fr.) Kummer" [= *Entoloma* Kummer].

**Syn.:** *Rhodogoniosporaceae* Heim, *Treb. Mus. Ciènc. Nat. Barcelona* 15: 86. 1934. (nom. nud.); Sing., *Ann. Mycol.* 34: 328, 323. 1936 (nom. subnud.).

*Jugasporaceae* Sing., *Ann. Mycol.* 34: 327, 323. 1936 (not valid).

*Clitopilaceae* Orton in Dennis, Orton & Hora, *Trans. Brit. Myc. Soc. Suppl.*, p. 6. 1960 (nom. nud.).

*Rhodophyllaceae* Sing., *Lilloa* 22: 601. 1949 (not valid).

**Characters:** Spore print pink (around, "French beige", or "woodland rose"; "rose beige", "rose beige 2+", "blush", or Pl. 12, D-8, Maerz & Paul); spores hyaline to pink-stramineous, inamyloid, angular in end-view (with the longitudinal axis vertical), or in all views, the angles often rather rounded, rarely so rounded that the spores do not appear angular any more, but then usually at least a few spores mixed in every print that show traces of an angular outline, cyanophilic, wall of mature spores off hyaline (usually pale pinkish stramineous) not quite thin, in EM sections showing a mediane layer between the smooth surfaces of the coriotunica and the surface layer (tectum). Not obligatorily ectomycorrhizal (but some species might be facultatively mycorrhizal).

**Limits:** The family Entolomataceae differs from all other groups of pink-spored agarics in having spores which are angular, sometimes only in polar view (because of longitudinal flat stripes alternating with rounded to acute ribs) and have a characteristically complex wall structure as seen in EM photos in section (see chapter XVIII2 and Pl. 53 A). The close relationship of all three genera has now been recognized by practically all modern authors. A certain degree of affinity may be seen in the similarity of the Entolomataceae e. gr. *Clitopilus* with *Pleurotellus* on one hand and *Paxillus* on the other but these similarities may be superficial and not phylogenetical. It is because of these similarities that I have inserted the Entolomataceae between the Crepidotaceae and the Paxillaceae; but it may be assumed that a closer

affinity exists between the Entolomataceae and the Tricholomataceae because the tribus Lyophylleae and Termitomyceteae, and some species of *Rhodocybe* and *Entoloma* have some type of siderophilous granulosity observable in the light microscope. A quantitative analysis using the Singer-Machol method based on Bayesian analysis has therefore been carried out, taking into account all characters of the families involved, with the result that the Entolomataceae are considerably more removed from the Lyophylleae than the other tribus of the Tricholomataceae. Furthermore, Pegler & Young have found that in the Entolomataceae thus far studied, the spores have a nodulose hilum whereas in Lyophylleae, they have an open-pore hilum. This result justifies the separation of the Entolomataceae from the Tricholomataceae on a family level. This is equally valid for the supposed affinity of other pink-spored families and genera and corroborated by Baroni's (1981, p. 125) statement: "I am not in agreement with Kühner's placement of the Entolomataceae in his order Pluteales along with the Pluteaceae and Macrocyptidiaceae ... A very near relation of the Entolomataceae may never be found in the extant members of the Agaricales". On the other hand, the gastromycetous affinities of the two families are evidently also different.

#### KEY TO THE GENERA

- A. Spores not or indistinctly angular in frontal view and in profile, but often rough or verruculose; hyphal elements of the stipe generally not cenocytic (Kühner 1958).
  - B. Spores smooth except for a slight unevenness produced by longitudinal ribs, or flattened "facades", i.e. an ornamentation of longitudinal ridges (type XII) or a combination of short ridges and warts in catenulation (type VIII-XII); pigments absent or scarce, sometimes gray; hyphae without clamp connections; cystidia and pseudocystidia generally absent      190. *Clitopilus* p. 699
  - B. Spores rough to  $\pm$  tubercular-warty when seen in profile or frontally; ornamentation of  $\pm$  isolated warts which are not longitudinally seriate and often very small, a median wall layer "stuffing" usually organized in a network; there exist occasionally a minority of spores somewhat angular in profile; pigments of the covering hyphal layers of the carpophores either absent or present, if present chemically and in color widely variable; hyphae with or more commonly without clamp connections; cystidia and/or pseudocystidia often present      191. *Rhodocybe*, p. 702
- A. Spores angular in frontal view and in profile, not rough or verrucose; hyphal elements of the stipe generally (or mostly) multinucleate to cenocytic (Kühner 1958).      192. *Entoloma*, p. 705

#### 190. CLITOPILUS Kummer

*Führ. Pilzk.*, p. 23. 1871.

*Type species: C. prunulus* (Scop. ex Fr.) Kummer.

*Syn.: Agaricus tribus Mouceron* Fr., *Syst. Mycol.* 1: 193. 1821.

*Agaricus tribus Clitopilus* Fr., *Epicrisis*, p. 148. 1838; *Monogr.* 1: 279. 1854.

*Clitopilus* (Fr.) Quél., *Champ. Jura Vosg.*, p. 85. 1872-3.

*Hexajuga* Fayod, *Ann. Soc. Nat., Bot.* VII. 9: 389. 1889.

*Octojuga* Fayod, l.c., p. 390.

*Orcella* Batt. ex Earle, *Bull. N. Y. Bot. Gard.* 5: 430. 1909.

*Pleoporus* Roussel ex Murr., *N. Am. Fl.* 10: 102. 1917, non (Pers. ex) S.F. Gray (1821).

**Characters:** Pileus subglabrous to sericeous, smooth or more rarely venose, not viscid or scarcely viscid, small to rather large, the margin initially frequently involute, the color here as in the whole carpophore usually very pallid, i.e. mostly white or whitish, more rarely light gray, or with a creamy ochraceous hue; epicutis consisting of repent, filamentous, hyaline, smooth thin hyphae (Pl. 75,11); spore print pink e. gr. between "sundown" and "cork" (Maerz & Paul) in *C. hobsonii*; hymenophore very rarely poroid rather than lamellate, but normally lamellate in all species; lamellae decurrent (where there is a distinct, persistent stipe); basidia normal, but rarely 1-3-spored, most frequently, however, 4-spored, and in most individuals at least some basidia 4-spored (Pl. 75,10); cystidia none on the sides of the lamellae; cheilocystidia also scarcely differentiated; however, there is often a large number of abnormal basidia (cystidioles) which do not become individualized enough to be of taxonomic interest; hymenophoral trama consisting of a mediostratum of more or less interwoven, subregularly arranged hyphae, with a generally axillar trend, and a lateral stratum (or more correctly hymenopodium) which is not sharply differentiated from the mediostratum, differing by the gradually larger volume of hyphae as they approach the subhymenium; hyphae looser in the mediostratum, and more interwoven away from the edge of the lamellae, hyaline; spores (Pl. 10; 75, 8-9) hyaline to usually pale stramineous under the microscope, with 5-10 longitudinal ridges, or angles at the borderline between each of the two of the flattened stripes ("facettes") running along the sides of the spores, otherwise smooth, without germ pore and without callus, with rather thin and very easily collapsing walls, young spores less distinctly angular, ovoid, ellipsoid-fusoid, always asymmetric (heterotrophic); neither amyloid nor pseudoamyloid; stipe present or absent, if present, often short and inconspicuous or not persistent at maturity; often arising from a mat of mycelium, or a velutinous basal mycelium, without pseudorrhiza, without veil; odor often farinaceous; taste mild or bitter; tramal hyphae rather loosely arranged because of a very slight gelatinization of the entire trama as in the boletes; consequently, the context remarkably soft and tender; all hyphae without clamp connections (Pl. 75,11); nonamyloid. On various dead and living plant material, on dead insects, sand and humus, mosses, etc.; often in lawns and open woods on the ground, and more often on wood, but also on such substrata as dung, ant-site, etc.). All species homothallic according to Kühner & Vandendries. Chemical reactions weak or none.

**Development of the carpophores:** Gymnocarpous; stipitocarpous (Watling), at least in some species.

**Area:** Cosmopolitan.

**Limits:** The genus *Clitopilus* is easy to recognize for anyone who takes the trouble of checking on the peculiarly shaped spores, the lack of clamp connections, and the sericeous cutis on the pileus. It is close to no other genus except *Rhodocybe*, and there most species are colored, or very bitter. It is less close to *Entoloma* but has spores which are never angular when seen in profile or in frontal view.

Fayod originally distinguished two genera, *Octojuga* and *Hexajuga*, and the combination of both these genera into a single one produced the modern genus

*Clitopilus*. The author separated *Hexajuga* from *Octojuga*, just as Fayod did, until, in 1942, he found that there are species intermediate between the two genera, and consequently no sharp dividing line can be discovered. He then joined Josserand who, somewhat earlier, had indicated the same opinion.

*State of knowledge:* The genus *Clitopilus* has been studied by two authors independently, neither knowing of the other's work. Consequently, the general state of knowledge is comparatively satisfactory. We know now thirteen species in this genus.

*Practical importance:* Some of the larger forms are often eaten. *Clitopilus prunulus*, though bitter forms are sometimes encountered, is one of the best edible mushrooms. None of the *Clitopili* can be considered mycorrhizal on the basis of known facts or field observations. The wood-destroying qualities of some species are practically negligible. *C. passeckerianus* is a weed fungus in beds of the Cultivated Mushroom (*Agaricus bisporus*), but hardly damaging. "*Pleurotus mutilus*" (if this refers to the pleurotoid variety of *C. scyphoides* rather than to *Clitocybe josserandii* = *Pleurotus mutilus* sensu Joss.) contains an antibacterial substance, mutilin, according to Uhrova-Hejtmankova, Česk. Myk. 8: 70, 1954. An antibiotic pleuromutilin, has been indicated in *C. passeckerianus* and occurs probably also in other species (cf. Anke, Zeitschr. Mykol. 44: 136. 1978). *C. intermedius* Romagnesi (= *C. orcelloides*?) is said to contain small amounts of epimuscarin (*Helv. Chem. Acta* 59: 2434. 1976).

## SPECIES

Sect. 1. *CLITOPILUS* [Prunuli (Quél.) Sing.]. Carpophores medium to rather large, distinctly and persistently stipitate; spores with mostly six reinforced longitudinal angles, 10-14  $\mu\text{m}$  long. Hyphae not metachromatic in cresyl blue mounts.

*Type species:* *C. prunulus* (Scop. ex Fr.) Kummer.

*C. prunulus* (Scop. ex Fr.) Kummer [Paxillus, Quél. 1886; Hexajuga, Fayod; Rhodosporus, Schröter in Cohn; Pleuropus, Murr.; Paxillopsis, Lange; Clitopilus orcellus (Bull. ex Fr.) Kummer; Pleuropus obesus Murr.] with a bitter tasting variety.

Sect. 2. *SCYPHOIDES* Sing. (1946). Carpophores rather small to small, scarcely medium sized, or else spores smaller than 10  $\mu\text{m}$  in length; constantly and distinctly stipitate although stipe often eccentric; hyphae metachromatic in cresyl blue (Kühner & Romagnesi).

*Type species:* *C. scyphoides* (Fr.) Sing. (var. *typicus* f. *typicus* Sing.).

*C. giovanellae* (Bres.) Sing. (Omphalia, Bres.); *C. scyphoides* (Fr.) Sing. (sensu Lundell & Nannfeldt) (Omphalia, Kummer; Agaricus mutilus Fr. sensu Fr., Lange, non Josserand; Pleurotus, Gillet; Clitopilus submicropus Rick; Omphalina floridana Murr.; Pleuropus minimus Murr.; Clitopilus cretaceus R. Maire), with var. *scyphoides* and several varieties (see *Farlowia* 2: 554-557, 1946); *C. hrbanovi* (Vel.) Sing. (*C. omphaliformis* Joss.); *C. orcelloides* Pat. & Demange; *C. apalus* (Berk. &

Br.) Petch (Lentinus, Berk. & Br.); *C. pusillimus* (Speg.) Sing. (Omphalia, Speg.); *C. crispus* Pat. (unless too close to *C. apalus*).

Sect. 3. *PLEUROTELLOIDES* Sing. (1943). Stipe inconstant, or not persistent, or rudimentary, or completely lacking. Otherwise much like sect. 2.

Type species: *C. pleurotelloides* (Kühn.) Josserand.

*C. venososulcatus* Sing.; *C. incrustatus* Sing.; *C. hobsonii* (Berk. & Br.) Orton [Pleurotus, Sacc.; Pleurotus septicoides Henn.; Clitopilus Sing.; Clitopilus pleurotelloides (Kühn.) Josserand; Octojuga Kühn.; Octojuga fayodii Konr. & Maubl.; Geopetalum viticola Murr.; Pleurotus Coker; Crepidotus subversatus Peck apud Reid nom. nud.; Pleurotus pusillus Speg.; Pleurotus romellianus Pilát; Crepidotus funalis Rick]; *C. passeckerianus* (Pilát) Sing. (Pleurotus, Pilát; Pleurotus, Konr. & Maubl.; Octojuga, Sing. 1942); *C. rhodophyllus* (Bres.) Sing. (Pleurotus, Bres.); *C. argentinus* Sing. [Pleurotus pusillimus Speg. non Clitopilus pusillimus (Speg.) Sing.]; *C. rhodotrama* Sing.

## 191. RHODOCYBE R. Maire

Bull. Soc. Mycol. Fr. 40: 298. 1925; em.

Type species: *R. caelata* (Fr.) R. Maire.

Syn.: *Clitopilopsis* Maire, Publ. Inst. Bot. Barcelona 3(4): 82. 1937.

*Hirneola* Velen., Nov. Myc., p. 73. 1939 non Fr. (1849).

*Pluteospora* Maire, Bull. Soc. Mycol. Fr. 50: xxvii 1934 (publ. March 1935) (nom. nud.).

*Rhodophana* Kühn. ex Métrod, Rev. Mycol. 17: 69. 1952.

Characters: Habit variable: collybioid, mycenoid, omphalioid, clitocyboid, tricholomatoid, or pleurotoid; pileus pigmented or not; epicutis consisting of filamentous hyphae forming a cutis, these hyphae parallel or subparallel with each other, radially arranged, sometimes some superficial hypha ends ascending, but in a few species forming a distinct trichodermium; hymenophoral trama strictly regular, consisting of long filamentous hyphae, more rarely ± strongly inflated parallel or subparallel with each other; lamellae adnexed, adnate, or decurrent, sometimes rounded to sinuate, sometimes initially ascendant; basidia normal, usually without siderophilous granulation, not excessively long, generally 4-spored, more rarely a minority (1)-2-(3)-spored; cheilocystidia differentiated, or absent; pleurocystidia differentiated, or absent; pseudocystidia on the sides of the lamellae continuing or not a system of conducting elements, often strikingly colored, present in one section (*Rhodocybe*), not gloeocystidioid nor macrocystidioid, not laticiferous; spore print pink to sordid gray, varying from very pale (2-A-8 of Maerz & Paul) to color of spore print of *Entoloma*, or more gray (in *R. hirneola* and *R. griseospora*); spores hyaline to pale stramineous, sometimes with a fuscidulous shade, with the hilum of the nodulose type, rough-warty-spinulose (or a minority or, among young spores, a majority almost smooth), strongly angular to rounded-angular in polar view, and only a minority of the spores showing a somewhat

angular outline when seen in profile with a continuous layer of cyanophilic wall material, rarely, especially young spores with circular outline in polar view; stipe present, generally central (excepting sections *Claudopus* and *Crepidotooides*); veil none; context consisting of clamp-less, rarely clamped, inamyloid hyphae and occasional oleiferous hyphae. On the ground, more rarely on dead wood or débris.

*Development of the carpophores:* Perhaps gymnocarpous in most species, but described in *R. mundula* as if it were vaguely pseudoangiocarpous (pilangiocarpous in the terminology of Reijnders) by Blizzard (1917).

*Area:* Temperate and subtropical as well as tropical zones of both hemispheres, in South America from the tropical rain forest of the Amazonas up to the alpine zone of the Andes, also in *Nothofagus* zone.

*Limits:* In the present circumscription (Singer 1946), this genus is clearly separated from the other genera of Entolomataceae by the spore characters stressed in the key.

The genus has in the past often been confused with *Lepista*. As a general rule, those species with clamp connections and uninucleate spores belong in *Lepista* rather than *Rhodocybe*. However, *R. nitellina* (Fr.) Sing. sensu Romagnesi, Kühner non Höhnel, Singer, has, according to Kühner, clamped hyphae and uninucleate spores but this species is recognizable as a *Rhodocybe* - aside from the collybioid habit - by the spore wall structure which is continuously cyanophilic (in contrast to the spores of *Lepista* which have only cyanophilic warts) and, according to the photos from EM preparations (Besson, *C.R. Acad. Sc. Paris* 269: 142-145. 1969), of the *Rhodocybe*-type.

*Lyophyllum* differs from *Rhodocybe* by showing another type of siderophilous basidia and by a hilum of the open-pore type according to Pegler (see also note under *Lyophyllum* subgenus *Lyophyllopsis*, p. 220). Baroni & Bigelow (1977) and Baroni (1981) seem to exclude all species with any siderophilous granulation in the basidia and wish to include them "in or near *Lyophyllum*". However, some type of siderophilous granulation has been observed in *Entoloma*. Spores with angular outline in polar view are definitely present in the types of *L. leucopaxilloides* and *L. suburens*.

*State of knowledge:* The exploration of the Rhodocyes in tropical and subtropical America has contributed much to obtain a better idea of the scope of the (originally monotypic) genus and its species as well as the infrageneric classification. 30 species are here recognized. The genus is now rather well known thanks to a world monograph (Baroni, *Nov. Hedw. Beih.* 67. 1981).

*Practical importance:* Some species are edible.

## SPECIES

Sect. 1. *RHODOPHANA* (Kühn.) Sing. (1972). Clamp connections present; collybioid.

*Type species: R. nitellina* (Fr.) Sing. sensu Romagnesi, Kühner.

*R. nitellina* (Fr.) Sing.; *R. lignicola* Sing.; *R. mycenoides* Sing.; according to Baroni also seven other species including *R. stangiana* (Bresinsky & Pfaff) Riousset & Joss. (*Squamanita*, Bresinsky & Pfaff)

Sect. 2. *RUBROBRUNNEA* Baroni\* (1981). External appearance somewhat like *Hebeloma*, *Collybia*, or *Tricholoma*, more rarely of *Mycena* or *Clitocybe gibba* or *Lepista gilva*; pileus rusty orange, fulvous, deep cinnamon-fulvous, brownish yellow, tan color, etc. Taste more often mild than bitter; pseudocystidia none; clamp connections none.

*Type species: Rhodopaxillus nitellinus* (Fr.) Sing. (sensu Sing.).

1. Species of the northern extratropical and subtropical zone (all without siderophilous granulation in the basidia).

*R. roseavellanea* (Murr.) Sing.; *R. truncata* (Schaeff. ex Fr.) Sing. (*Hebeloma*, Kummer; *Agaricus subbalteatus* Fr. ex Secr. non Fr. ex Fr., with three subspecies: *truncata*, *mauretanica* (Maire) Sing. and *subvermicularis* (Maire) Sing.); *R. alutacea* Sing.; *R. nuciolens* (Murr.) Sing.; *R. nitellina* (Fr.) Sing. (sensu Sing. non Romagnesi, Kühner (if not identical with a validly described species); obviously also *R. pascuensis* (Peck) Baroni and *R. hondensis* (Murr.) Baroni).

2. Species of the neotropics without cystidia on the sides of the lamellae:

*R. laeta* Sing.; *R. marasmoides* Sing.; *R. testacea* Dennis; *R. rickii* Sing. (with var. *rickii* and var. *convexa* (Sing.) Sing.); *R. collybioides* Sing.\*\*; *R. pseudonitellina* Dennis.

3. Other species.\*\*\*

According to Baroni: *R. subgilva* (Br. & Br.) Pegler and *R. piperita* (Stevenson) Horak.

Sect. 3. *DECURRENTES* (Konr. & Maubl.) Sing. (1951). Pileus whitish and not tending to become gilvous in parts, or gray to fuliginous-fuscous; habit omphaloid or clitocyboid; pleurocystidia present or absent, but pseudocystidia none.

*Type species: Rhodopaxillus mundulus* (Lasch) Konr. & Maubl.

1. Species with spores not showing a fuscous shade in water mounts, pink in print:

*R. mundula* (Lasch) Sing. [*Rhodopaxillus*, Konr. & Maubl.; *Rhodocybe noveboracensis* (Peck) Sing.; *Clitopilus*, Sacc.]; *R. popinalis* (Fr.) Sing. (*Clitopilus*, Kummer); *R. fallax* (Quél.) Sing. (*Omphalia*, Quél.; *Clitocybe*, Sacc. & Trott.); *R.*

\*“*RUFROBRUNNEA*”, apparently an unintentional spelling error.

\*\*Possibly to sect. *Rhodocybe*, but type described as acystidiate.

\*\*\*As for species with siderophilous granulation in the basidia (*R. smithii* Harmaja, *R. suburens* (Cléménçon) Sing. & Clém., *R. leucopaxilloides* (Smith & Bigelow) Sing. (further studies are necessary (see also under *Lyophyllum*, p. 220-221)).

*parilis* (Fr.) Sing. (Clitocybe, Gillet; Omphalia, Quél.); *R. himantiigena* (Speg.) Sing. (Clitocybe, Speg.); *R. semiarboricola* Baroni.

2. Species with spores showing a fuscous shade in water mounts, almost gray in print, with firm walls:

*R. hirneola* (Fr.) Orton\* (Clitocybe, Kummer; Clitopilus, Kühn. & Romagnesi, Clitopilopsis, Konr. & Maubl.).

3. Species with  $\pm$  pinkish spore print and tomentose pileus (sect. *Tomentosae* Baroni ("Tomentosi"), with *R. sphaerospora* (Peck) Baroni as type species).

*R. sphaerospora* (Peck) Baroni and *R. lutetiana* (Gilbert) Bon apud Bon & Chevassut, both according to Baroni, unknown to me.

Sect. 4. *CLAUDOPODES* Sing. (1961). Like sect. 1 and 2, but with pleurotoid habit. Alpine species (South America).

*R. claudopus* Sing.

Sect. 5. *RHODOCYBE* (*Genuinae* Sing. 1946). External appearance sometimes of a small *Tricholoma* or *Clitocybe*, sometimes of a small *Lepista*, rarely of a *Galerina* or a *Lactarius* (*Russulariae*), sometimes somewhat eccentric; with striking pseudocystidia, these generally colored, many continued into the conducting system of the trama where the conduction elements are also usually colored (NH<sub>4</sub>OH) but not staining blue in cresyl blue mounts (i.e. they are not gloeo-vessels), or with conspicuously incrusted cystidia, the cystidial contents taking up alkalic Congo red solution.

Type species: *R. caelata* (Fr.) Maire.

*R. caelata* (Fr.) Maire (Tricholoma, Gillet; *R. dubia* Favre); *R. galerinoides* Sing.; *R. naucoria* Sing.; *R. russularia* Sing.; *R. lactariiformis* Sing.; *R. caelatooides* Dennis; obviously also *R. arenicola* (Karst.) Lange & Silvertsen (Omphalia, Karst. - if different from *R. caelata*); obviously also *R. griseospora* (Peersch) Orton (drab-spored).

Sect. 6. *CREPIDOTOIDES* Sing. (1972). Like section 5, but habit a pleurotoid.

Type and only species: *R. crepidotooides* Sing.

## 192. ENTOLOMA Kummer

Führ. Pilzk. p. 23. 1871.

Type species: *Entoloma sinuatum* (Pers. ex Fr.) Kummer.\*\*

\*In the sense of Kühner & Romagnesi, Horak, Singer the spore print is grayish (= *Clitopilopsis arthrospora* Kühner); as described by Baroni (1981) the spore print is pinkish. Also, the spores of the gray-spored species are smaller. It is possible that the latter should be called *R. parilis* (Fr.) Sing. but Baroni points out that the latter needs typification by a holotype. He seems to believe that the gray and the pink-spored *R. hirneola* are conspecific.

\*\*There is no valid objection against Donk's first choice (for *Entoloma* "(Fr.) Kummer" which is also that of Singer (1936) and Clements & Shear (1931)).

Syn.: *Acurtis* Fr., *Summa Veg. Scan.* p. 337. 1849.\*

*Eccilia* Kummer, *Führ. Pilzk.* p. 23. 1871.

*Agaricus* trib. *Eccilia* Fr., *Syst. Myc.* 1: 207. 1821.

*Eccilia* (Fr.) Quél., *Champ. Jura Vosg.* p. 123. 1972-3.

*Agaricus* tribus *Entoloma* Fr., l.c. p. 143.

*Entoloma* (Fr.) Quél., l.c., p. 116.

*Nolanea* Kummer, l.c., p. 24.

*Agaricus* tribus *Nolanea* Fr., l.c., p. 204.

*Nolanea* (Fr.) Quél., l.c., p. 122.

*Leptonia* Kummer, l.c.

*Agaricus* tribus *Leptonia* Fr., l.c., p. 201.

*Leptonia* (Fr.) Quél., l.c., p. 121.

*Agaricus* subgen. *Claudopus* W.G. Smith, *Clavis Agar.*, p. 17. 1870\*\*, *Journ. Bot.* (Seemann) 8:

215, 1870; tribus, Fries, *Hym. Eur.* p. 213. 1874.

*Claudopus* (Fr.) Gillet, *Champ.*, p. 426. 1876.

*Rhodophyllus* Quél., *Enchirid.* p. 57: 1886 (superfluous name).

*Hyporrhodius* Schröter in Cohn, *Krypt.-Fl. Schlesien, Pilze* 1: 613. 1889.

\*According to the present Code of nomenclature the correct name for this genus is *Acurtis*. *Entoloma giganteum* occurs in two fructification forms usually occurring together as shown on pl. 7, more rarely exclusively in one or the other form. Both forms when mature produce basidia and basidiospores. In the *Acurtis*-form (*Acurtis gigantea* Fr., the type species of *Acurtis*), the basidia are "endobasidia" and they are not numerous; therefore, they have often been overlooked since the material sectioned either was too young to show them, or the sectioning too limited (there is no macroscopically visible fertile zone). Consequently, the fact that basidia have not been found in the type specimen (Schweinitz Herbarium) by me or by Hesler does not prove that my observation made on numerous collections from many parts of North America is incorrect and even less that it is an imperfect state of *C. abortivus*. *Acurtis* is also by no means a monstrosity as the term is widely understood unless we accept Watling's (1974) suggestion that the "aborted" carpophores are parasitized by *Armillariella*. This would assume that (1) his observations prove to be correct (2) that they may then be interpreted as monstrosities. It is correct to indicate that in *Acurtis*-forms frequently endobasidia are formed which do not form *Entoloma* spores but *Armillariella* spores, or what looks very much like *Armillariella* spores. I have myself observed that in most collections at least some of the *Acurtis* carpophores contain such basidia and spores and that wherever *Acurtis* forms occur, *Armillariella polymyces* - ordinarily later-fruiting - occurs nearby. This makes Watling's observations very probable and since they are thus far the only and best explanation of the phenomenon, quite acceptable. If, then, we go one step further, and consider the incapacity of the infected carpophores to form agaricoid (lamellate) stages as representing a monstrosity (Art. 71) we still have not solved the problem of the nomenclaturally correct generic name of one of the largest genera in Agaricales. Less probable is application of the (former) article 70 for "nomina ambigua" since the type apparently does not contain other hyphae than those of the host, and a typification in the sense of *Entoloma* is perfectly possible.

In order to avoid the replacement of either *Rhodophyllus* or *Entoloma*, the conservation of *Rhodophyllus* Quél. with the type species *R. parkensis* has been proposed repeatedly, and the necessity of conserving *Entoloma*, in case of rejection of *Rhodophyllus* as conserved name, has been suggested (e. gr. 3rd ed. of this work, 1975, p. 673). Under these circumstances, it is tragicomical to see that the same (Leningrad) Congress which rejected the conservation of *Rhodophyllus* deleted Art. 70 and 71, the only articles in the Code that might have saved *Rhodophyllus* and/or *Entoloma*!

With a strict application of the rules as given in the latest (1983, "Sydney"-) Code, *Acurtis* is obviously still a valid, legitimate name, and being the oldest for the genus here treated as *Entoloma*, should replace it, with hundreds of new combinations required. The lesson to be learned from this is (1) *Entoloma* should be accepted as nomen conservandum against *Acurtis* and other generic names (2) Machol's article ("Leave the Code alone", *Taxon* 33: 532-533. 1984 and Johnston's proposal 39, *ibid.* p. 535 as well as Dörfelt's (*ibid.*, p. 533) should be heeded.

\*\*Donk states that "this genus was established with *Agaricus euosmus* Berk. as the type species by original designation". This is not so as can easily be checked by whoever takes the trouble to look up the original diagnosis.

- Latzinaea* O. Kuntze, *Rev. Gen. Pl.* 2: 857. 1891.  
*Leptoniella* Earle, *Bull. N. Y. Bot. Gard.* 5: 424. 1909.  
*Lanolea* Nieuwland, *Ann. Midl. Nat.* 4: 381. 1916.  
*Arenicola* Velen., *Nov. Mycol. Nov.* p. 62. 1947.  
*Pouzaramyces* Pilát, *Sborn. Narodn. Mus. Praze* 9B(2): 60. 1953.  
*Alboleptonia* Largent & Benedict, *Mycologia* 62: 439. 1970.  
*Pouzarella* Mazzer, *Bibl. Mycologica* 46: 69. 1976.

**Characters:** Spores (Pl. 12,1; 16; 53A) with moderately thick to rather thin, simple, inamyloid cyanophilic wall, usually angular and then with angular outline from all sides, from the ends (with the longitudinal axis vertical) as well as in profile, or frontally, pink in print ("rose beige 2+" to "blush", or Plate 12, D8 reaching "brick red" to "Pecan br." of Maerz & Paul); basidia normal or with siderophilous granulosity, rather rarely 2-spored, but definite 2-spored races are in existence; cystidia absent or present, either only on or near the edges of the lamellae, or on the sides as well as on the edges; hymenophore lamellate in all normal forms; hymenophoral trama regular in the mediostratum, irregular and denser in an outer layer (hymenopodium); subhymenium consistently of very short elements; habit pleurotoid, mycenoid, collybioid, omphaliod, clitocyboid, or tricholomatoid; lamellae never quite free as in the Amanitaceae; hyphae inamyloid, with or without clamp connections, sometimes intermixed with laticiferous hyphae; veil none, or fugacious (traces of a cortina); latex present in one species. On various substrata, even on carpophores of Agaricales and Aphyllophorales, also in deep moss, on cortex and wood, dead leaves, etc., most frequently on the soil, not ectomycorrhizal. It is, however, possible that some species of the genus are facultatively ectomycorrhizal as might be deduced from the laboratory synthesis of *Salix rotundifolia/Entoloma sericeum* accomplished by Linkins & Antibus (*Arct. and Alpine Mycology* 5, p. 518. 1980).

**Development of the carpophores:** Gymnocarpous in the species studied by Douglas and Blizzard; pileostipitocarpous in species studied by Watling (1985).

**Area:** Cosmopolitan, but most of the single species occupying very definite areas, and even some of the sections predominantly either temperate or tropical, etc.

**Limits:** The delimitation of the genus is less difficult with regard to the other two genera of the family than concerning the possibility of it being split up into several genera, either according to the groupings accepted by Fries and his school, or according to more modern principles (such as stressed by Largent & Benedict). As for the Friesian tribus elevated to genera by Kummer and Gillet, I agree with Kühner & Romagnesi who took up Quélet's genus *Rhodophyllus* for the entire group (as did Quélet, Lange, Romagnesi and the present author, followed by A.H. Smith, and other American authors (excepting Hesler) and the Japanese mycologists, as well as the majority of the Europeans with the exception of some recent, mainly British authors; but even in the case of those who did recognize *Claudopus*, *Eccilia*, *Nolanea*, *Leptonia*, and *Entoloma* it may well be that the unsettled question of the legal name for the combined genus is at least one of the motives determining the taxonomic solution. The split genera resulting from the research of Largent & Benedict are a different matter. It seems to me that the resulting small genera are based

on too small a percentage of the species referable to *Rhodophyllus*, and even if tenable after a majority of the species have been checked for the characters emphasized by these authors, they do not seem to be - according to my own relatively limited experience - on the same level as the two genera now recognized - *Rhodocybe* and *Clitopilus*. It should also be taken into consideration that further, obviously important characters such as the chemical reactions with certain organic reagents on the carpophore as well as the siderophilous granulation and its different types, have not been investigated in a sufficient number of species. Nevertheless, the subdivision of the whole *Rhodophyllus* complex as attempted by Largent & Benedict is in my opinion an important step which may lead to better defined groupings, irrespective of the status of the taxa resulting.

Other species with angular spores, belonging to the Tricholomataceae, Agaricaceae, or Cortinariaceae have spore walls not showing the characteristic ultrastructure (cf. chapter XVIII, pl. 53A) of *Entoloma* spores, and, in addition, some of them differ in a sporal hilum of the open-pore type. Besides, their spore print color is not pinkish.

*State of knowledge:* It is obvious from what has been said above that the "final" classification of *Entoloma* and the number of species to be recognized in the end depends on extensive monographic work including many data now not available. More than 600 species have been described in *Entoloma* (respectively in the genera here indicated as synonyms).

Out of this total 89 species are here given as examples for the various infrageneric taxa here recognized. As far as the latter are concerned, we are confronted in the literature with a bewildering and widely discrepant array of schemes, reflecting the views of modern specialists such as Romagnesi (1941), Singer (1951), Kühner & Romagnesi, a revised taxonomic outline by Romagnesi (1978), Hesler, Largent & Benedict, and Noordeloos (1981), some of them dividing the genus into several genera, others treating them under a single generic name which is variously given as *Rhodophyllus* (by Romagnesi, Singer), *Entoloma* (Hesler, Noordeloos) and tentatively as *Acurtis* which indeed, as we have shown (see p. 706, footnote \*), is the correct name if the present rules are strictly applied. But for merely practical reasons, and in view of further changes in the Code dictated by a wish to adapt the rules to the aims of the Code, not vice versa, I cannot propose to transfer over 600 epithets from half a dozen of genera, mostly widely used ones, to *Acurtis*. On the other hand, it does not appear to me that the Friesian tribus *Eccilia*, etc. are genera on the same level as *Rhodocybe* and *Clitopilus*.

Under these circumstances, I believe that *Entoloma* represents at present - not when the conservation of *Rhodophyllus* was first proposed - the most widely used generic name for the group sensu lato, and its conservation should be proposed and accepted if no other manner of excluding *Acurtis* can be introduced in the rules as they will emerge from the Berlin Congress.

The most acceptable infrageneric classification now available is in my opinion that

of Noordeloos. His classification, with few minor modifications, is used in the following enumeration of the species.

The reasons for this decision are several, one of them being the fact that in the same year 1978 Romagnesi abandoned the application of his scheme of spore shape types as primary and decisive character for the taxonomy in *Rhodophyllus* (*Entoloma*) and Pegler & Young introduced a new, obviously more precise and elaborate system of spore morphology in the genus. A general coordination between their findings and the accepted subgeneric taxa has thus far not materialized but will probably play a certain role in further definition of these taxa, or lead to the introduction of additional ones.

**Practical importance:** Some species are edible. A few are even sold in the markets of Europe and Asia. For every good edible species there seems to be one poisonous species. Among them, *E. sinuatum* is a truly dangerous species. Other poisonous species occur in the group of *R. rhodopolius*. In both these cases muscarin and/or its stereomer epimuscacin are present (see Stadelmann et al., *Helv. Chim. Acta* 59: 2436. 1976). Furthermore, *E. sericeum* and *E. vernum* as well as *E. niphoides* have been indicated as being poisonous.

## SPECIES

**Subgenus I. Entoloma.** "Carpophores usually tricholomatoid, rarely collybioid or clitocyboid, mycenoid or omphalioid; pileus usually conico-convex then flattened with or without broad umbo, rarely entirely flattened, cup-shaped or with central depression, hygrophanous or not, smooth or radially fibrillose, never fibrillose-squamulose; lamellae usually deeply emarginate or adnate, rarely adnate-subdecurrent; stipe usually aeriferously-fibrillose striate lengthwise, rarely smooth as if polished; spores often more or less isodiametrical, with basal facet or blunt dihedral base; pileipellis a cutis or ixocutis made up of cylindrical hyphae, sometimes with ascending, clavate terminal cells. Pigment usually intracellular, rarely membranal or incrusting. Hymenophoral trama and pileitrama regular, made up of chains of relatively short (on the average 40-150  $\mu\text{m}$  long) cylindrical or inflated cells; clamp-connections usually abundant in all parts of the carpophore." (Noordeloos).

**Type species:** *Entoloma sinuatum* (Pers. ex Fr.) Kummer.

Sect. 1. *ENTOLOMA*. (*Agaricus* sect. *Genuini* Fr.; *Rhodophyllus* sect. *Madidi* Romagn.). Habit tricholomatoid; pileus not hygrophanous; margin of pileus non-striate; pigments gray, brown, blue or green or none; epicutis in form of a cutis or ixocutis, with intracellular pigments or hyaline. Often poisonous. (Noordeloos).

**Type species:** *E. sinuatum* (Pers. ex Fr.) Kummer.

*E. sinuatum* (Pers. ex Fr.) Kummer; *E. lavidum* (Bull. ex St-Amans) Quél. (*Agaricus*, Bull. ex St-Amans, Mérat non Pers. ex Schwein., Secr.); *E. prunuloides* (Fr.) Quél. - Apparently also *E. madidum* (Fr.) Quél. and *E. viridans* Karst.; many of the extra-European species, e. gr. *E. lilacipes* Horak and *E. lyophylliforme* (Sing.)

Horak differ in absence of clamp connections. These species may require a separate section.

Sect. 2. *NOLANIDEA* (Fr.) Quél. (1872). Much like the preceding and the following section but pileus either non-hygrophanous or hygrophanous, and fungi combining the presence of an ixocutis with farinaceous taste and strictly vernal fruiting; pileus white, grey, yellowish or brownish to dark brown or fuscous, sometimes with an olivaceous tinge; pigments intracellular or absent. Often poisonous, mostly temperate species.

*Type species: Agicus clypeatus* L. ex Fr.

*E. clypeatum* (L. ex Fr.) Kummer; *R. aprile* (Britz.) Sacc., and several other, mostly temperate species.

Sect. 3. *RHODOPOLIA* (Fr.) Noordeloos (1981). Habit tricholomatoid, more rarely slender and almost mycenoid; pileus white, yellow, brown, fuscous, or gray, hygrophanous; pigment intracellular or incrusting, or both; summer-fall fruiting species. Often poisonous. (Noordeloos).

*Type species: Agaricus rhodopolius* Fr.

*E. rhodopolium* (Fr.) Kummer; *E. nidorosum* (Fr.) Quél. and several other species. Apparently here: *E. patagonicum* (Sing.) Horak.

Sect. 4. *POLITA* (Romagn.) ex Noordeloos. (*Eccilia* (Fr.) Kummer). Habit omphaloid or collybioid; pileus depressed or umbilicate, rarely papillaté in the center; lamellae adnate, uncinate, or decurrent; stipe smooth (as if polished); pigments intracellular; clamp connections abundant. (Noordeloos).

*Type species: Agaricus politus* Pers. ex Fr.

*E. politum* (Pers. ex Fr.) Donk; *E. sericatum* (Britz.) Sacc.; *E. alpicola* (Favre) Noordeloos ("alpicolum"); obviously also several other species according to Noordeloos.

Sect. 5. *ACURTIS* Sing.\* Habit clitocyboid; lamellae decurrent; stipe smooth; pigments intraparietal and incrusting; pileus not hygrophanous, not viscid; clamp connections absent; spores distinctly elongated.

*Type and only known species: E. giganteum* (Schwein.) Sing.\*\* (Acurtis, Fr.; Rhodophyllus, Sing.; Clitopilus abortivus (Peck) Sacc.; Entoloma, Donk).

Sect. 6. *CLITOPILOIDES* (Romagn.) Noordeloos (1981). Habit clitocyboid; pileus depressed, dark brown, [hygropanous], lamellae broadly adnate to subdecurrent; stipe fibrillosely striate longitudinally; spores subisodiametrical or cuboid; pigment intracellular; clamp connections absent. (Noordeloos).

\*sect. nov. Carphophoris clitocyboideis; pigmentis intraparietalibus praesentibus; pileo neque hygrophano nec viscidio; fibulis nullis; sporis elongatis. Typus: *E. giganteum* (Schwein.) Sing.

\*\*c.n. (*Acurtis giganteus* Fr., Summa Veg. Scan. p. 337, 1849). The new combination is made on the surmise that *Entoloma* will be legalized by conservation since the present Code does not provide for rejection of *Acurtis* (see foot note on p. 706).

*Type species: E. costatum* (Fr.) Kummer.

*E. costatum* (Fr.) Kummer; obviously also some other species, probably *E. cutifrac-tum* Horak & Sing.

Sect. 7. *TURFOSA* (Romagnesi) Noordeloos (1979). Habit tricholomatoid or collybioid; pileus distinctly hygrophanous, smooth, grey-brown or yellowish brown; lamellae often with gray or brown tinge; spores small (6-9  $\mu\text{m}$  long), rounded- and multi-angled in side view, subisodiametrical to slightly oblong in outline, with very thin wall, slightly cyanophilous; epicutis a cutis or ixocutis made up of narrow, cylindrical hyphae with intracellular pigment; clamp connections numerous. (Noordeloos).

*Type species: E. turbidum* (Fr.) Quél.

*E. turbidum* (Fr.) Quél. and some related varieties and species, probably including *E. perbrevisporum* (Sing.) Horak.

Subgenus II. *Nolanea* (Fr.) Noordeloos (1979). Habit mycenoid, rarely slenderly tricholomatoid or omphalioid; pileus conical to conico-campanulate, then expanding, usually with papilla, rarely depressed at centre; hygrophanous; mostly translucently striate when moist, smooth or slightly fluffy-rugulose at centre; lamellae almost free or narrowly adnate or emarginate, rarely with decurrent tooth; stipe slender, often more or less cartilaginous; spores variable in shape, (sub-)isodiametrical to heterodiametrical or cuboid or cruciform; cystidia present or not; pileipellis a cutis, often with a tendency to become a trichoderm at center of pileus because of ascending hyphal endcells; pigment intracellular or membranal or encrusting or in combinations of two of these types; hymenophoral trama and pileitrama made up of relatively long, cylindrical to fusoid cells, mostly between 150-450  $\mu\text{m}$  long; clamp-connections, if present, abundant in hymenium, but [often] elsewhere rare or entirely lacking. (Noordeloos).

*Type species: Agaricus hirtipes* Schum. ex Fr.

Sect. 8. *MAMMOSA* (Romagn.) Sing. c.n. (*Rhodophyllus* sect. *Mammisi* Romagn. 1937). Pigments encrusting, but also intracellular in hypodermium; cheilocystidia present; spores elongated with basal facet; clamp connections present in the hymenium. (Noordeloos).

*Type species: Rhodophyllus mammosus* (L. ex Fr.) Quél.

*E. hirtipes* (Schum. ex Fr.) Moser (*A. mammosus* L. ex Fr.).

Sect. 9. *STAUROSPORA* (Largent & Thiers) Noordeloos (1979). Spores cuboid or prismatic (cruciform-stellate); pigment intraparietal, encrusting, or intracellular.

*Type species: Nolanea staurospera* Bres.

*E. conferendum* (Britz.) Noordeloos (*Nolanea staurospera* Bres.) and some additional species.

*Note:* *E. dragonosporum* (Sing.) Horak and apparently *E. pinnum* (Romagn.) Dennis which were thought to belong to this section are intermediate between sub-

gen. I and II and should enter subgenus *Inocephalus* (spores digitate-angular; pigment intracellular; clamps numerous).

Sect. 10. *COSMEOECONEMA* (Largent & Thiers) Noordeloos (1981). Pigment incrusting, at least the narrowest hyphae of the epicutis and pileus trama, sometimes with intracellular pigment in addition (but the latter never dominant); clamp connections present; spores isodiametrical or elongated, never cuboid or pirsmatical; cystidia usually absent. (Noordeloos).

Type species: *E. sericeum* (Bull. ex Mérat) Quél.

*E. sericeum* (Bull. ex Mérat) Quél.; *E. nitens* (Velen.) Noordeloos (*E. permutatum* Horak); *E. juncinum* (Kühn. & Romagn.) Noordeloos; *E. vernum* Lundell; *E. palliatum* (Bres.) Dennis (non sensu Dennis) and probably *E. strictius* (Peck) Sacc. and *E. dissimile* (Sing.) Horak (although clamps at times scarce or absent).

Sect. 11. *FERNANDAE* Noordeloos (1979). Two types of pigment present; one incrusting the walls of most hyphae in epicutis and upper pileitrama, another intracellular and forming, sometimes agglutinated, granules or clots; spores 5-6-7 angled, with distinct dihedral base; clamp-connections absent. (Noordeloos).

Type species: *E. fernandae* (Romagn.) Noordeloos.

Aside from the type species, Noordeloos enumerates eight species belonging in this section, all unknown to me, but *E. atripes* (Dennis) Horak (*Rhodophyllus venezuelanus* Sing. non *E. venezuelanus* Dennis sec. Horak) appears to belong here.

Sect. 12. *ENDOCHROMONEMA* (Largent & Thiers) Noordeloos (1979). Pigment intracellular, sometimes membranal or both; spores heterodiametrical with dihedral bse; cheilocystidia present or not; clamp-connections usually present. (Noordeloos).

Type species: *A. cetratus* Fr. = *E. cetratum* (Fr.) Moser.

*E. cetratum* (Fr.) Moser; *E. solstitiale* (Fr.) Noordeloos; *E. mesites* (Sing.) Sing. (*Rhodophyllus mesites* Sing., Nova Hedw. Beih. 29: 342. 1969); *E. inutile* (Britz.) Noordeloos; *E. icterinum* (Fr.) Moser; also several species unknown to me, and possibly *E. sparsicystis* Horak & Sing.; *E. murinialbum* Horak & Sing., and *E. spineum* Horak & Sing. (hyphae clampless).

Subgenus III. *Pouzaromyces* (Pilát) Moser ex Noordeloos (1979) (*Pouzarella Mazzer* 1976). Habit mycenoid, or reminiscent of that of a species of *Inocybe*; pileus conical or campanulate, only slowly expanding, not hygrophanous, translucently striate at margin or not, with metallic sheen, strongly radially fibrillose, fibrillose-hairy or fibrillose-squamulose; lamellae adnate, emarginate or almost free, but then often with distinct decurrent tooth, usually very dark grey-brown; stipe filiform to cylindrical, concolorous with pileus or slightly paler, with fibrillose or arachnid covering; spores angular or gibbose, often large, 9-20 µm long, ellipsoid to elongate in outline, fairly thick-walled; basidia 4-spored, large, when dry frequently with dark brown intracellular pigment; cheilocystidia usually present; hymenophoral trama regular with well-developed subcellular hymenopodium; pileipellis more or less

trichodermal; pigment abundant, encrusting in trama and covering layers, sometimes intracellular in addition. (Noordeloos).

*Type species: Nolanea fumosella* (Winter) Lange sensu Pilát\* (= *N. strigosissima* Rea).

Sect. 13. *LUCTUARIA* (Romagn.) Sing. c.n. (*Rhodophyllus* sect. *Luctuarii* Romagnesi *Bull. Soc. Linn. Lyon* 43: 330. 1974) (Pouzarella sect. *Dysthales* Mazzer). Pileus fibrillose-hairy to fibrillose-squamulose. Epicutis a cutis with transitions to a trichoderm with long, septate, attenuate hairs; pigment incrusting; cheilocystidia if present subcylindrical, subglobular to clavate, usually brown-encrusted. (Noordeloos).

*Type species: Rhodophyllus babingtonii* (Blox. ex Berk. & Br.) Quél. sensu Kühn. & Romagnesi (= *Entoloma strigosissimum* (Rea) Noordeloos).

*E. strigosissimum* (Rea) Noordeloos; *E. squamifolium* (Murr.) Sing.;\*\* *E. crinipelloides* (Sing.) Sing.;\*\*\* *E. dysthales* (Peck) Sacc.; *E. homomorphum* (Romagn.) Sing.\*\*\*\* Noordeloos (1981) indicates four, Horak (as gen. *Pouzaromyces*) three (Argentine) additional species referable to this section.

Sect. 14. *VERSATILIA* (Romagn. ex Romagn.) Noordeloos (1979). Pileus micaeous-fibrillose to fibrillose-hairy; cheilocystidia lageniform; pigment intracellular in epicutis, incrusting in the trama of the pileus. (Noordeloos).

*Type species: Rhodophyllus versatilis* (Fr.) Quél. (= *Entoloma versatile* (Fr.) Moser ("versatilis").

*E. versatile* (Fr.) Moser; also several other species according to Mazzer as Pouzarella, 1976 and Noordeloos (1981).

Subgenus IV. *Allocybe* Noordeloos (1981). (*Rhodophyllus* sect. *Excentrici* Romagnesi 1974). Habit tricholomatoid; pileus conical or flattened, not hygrophanous, white or leather brown; epicutis a cutis made up of 8-20  $\mu\text{m}$  wide cylindrical or inflated hyphae; pigment membranal or encrusting; spores heterodiametrical with basal facet; elements of trama 90-320  $\mu\text{m}$  long, cylindrical to fusoid; clamp-connections present at base of basidia. (Noordeloos).

\*Pilát (1953, p. 59-61) does not indicate a holotype for his genus *Pouzaromyces*. He describes a species under the name of *P. fumosellus* but merely cites Pearson and Dennis for its identity and synonymy which in the protologue twice includes *Nolanea strigosissima* Rea and his description of the species as well as of the genus include only the characters of *N. strigosissima* with the exclusion of any element foreign to the present section *Pouzaromyces*. According to Art. 7.2 and 10.2 of the 1983 Code, the illustration serving as type of *N. strigosissima* Rea or the collection by Pouzar cited by are eligible as holotypes. I select the latter because the specimen is preserved (apparently at PR) and the specific description given obviously based on it. If Art. 10.1 of the "Sydney-Code" were interpreted in such a way as to accept generic types that were misdetermined by the original author of the genus whereby these misdetermined specific names are in obvious conflict with the protologue, a whole revolution in generic name-giving would be invited.

\*\*c.n. (*Crinipellis squamifolius* Murr., *N. Am. Fl.* 9: 288. 1915).

\*\*\*c.n. (*Rhodophyllus crinipelloides* Sing., *Nova Hedw.* 29: 75. 1978).

\*\*\*\*c.n. (*Rhodophyllus fumosellus* var. *homomorphus* Romagn., *Prodr. Fl. Myc. Madag.* II, *Rhodophyllus*, p. 150. 1941).

*Type species: E. excentricum* Bres.

Sect. 15. *EXCENTRICI* (Romagn.) Sing. (*Rhodophyllus* sect. *Excentrici* Romagn., *Bull. Soc. Linn. Lyon.* 43: 332. 1974). Characters of the subgenus; same type species.

*E. excentricum* Bres. (and two additional species according to Noordeloos).

Subgenus V. *Trichopilus* (Romagn.) Noordeloos (1980). Habit tricholomatoid. Pileus often umbonate, rarely flattened, not hygrophanous, silky shining, densely radially fibrillose to fibrillose-squamulose; epicutis a trichodermium made up of ascending bundles of cylindrical or fusoid terminal cells of the underlaying layer, up to 25  $\mu\text{m}$  wide with intracellular pigment; hymenophoral trama regular, made up of long, fusoid, up to 450  $\mu\text{m}$  long cells; clamp-connections usually abundant. Noordeloos).

*Type species: E. jubatum* (Fr.) Karst.\*

Sect. 16. *LEPTONIDEA* (Fr.) Quél. (1886, as sect. of *Rhodophyllus*). Characters those of the subgenus but (sub)capitate lageniform cheilocystidia present.

*Type species: Agaricus jubatus* Fr.

*E. jubatum* (Fr.) Karst.; *E. porphyrophaeum* (Fr.) Karst. and several other species including, perhaps, *E. conspicuocystidiosum* Horak & Sing. (without clamps).

Sect. 17. *EROPHILA* (Romagn.) Noordeloos (1980). Differing from the preceding section in absence of cheilocystidia; often fruiting in spring.

*Type species: E. erophilum* (Fr.) Karst.

*E. erophilum* (Fr.) Karst.; *E. plebejum* Kalchbr.

Subgenus VI. *Inocephalus* Noordeloos (1981). Habit mycenoid [with the habit often like *Inocybe* or *Hygrocybe conica*]; pileus conico-campanulate then expanding, never depressed, usually papillate, with radially fibrillose or adpressedly squamulose, velutinous or slightly rimose surface; lamellae free or narrowly adnexed, never decurrent; spores with dihedral base; pileipellis [almost cutiform], trichodermial or hymeniform; pigment intracellular (Noordeloos); spores symmetric (Romagnesi, Singer).

*Type species: Rhodophyllus inocephalus\** Romagn.

Sect. 18. *INOCEPHALA* (Romagn. 1974) Noordeloos (1983). Pigment vacuolar; (pleuro-)pseudocystidia present; clamp connections typically absent. (Romagnesi). Aspect of *Inocybe*.

*Type species: Rhodophyllus inocephalus* Romagn.

*E. inocephalus* (Romagn.) Dennis (*Rhodophyllus*, Romagn.); *E. ferrugineogranulatum* (Sing.) Horak; *E. cystidiophorum* Dennis; probably also *E. cryptochroum* (Sing.) Horak.

\*Selected (Singer 1951).

Sect. 19. **CALLIDERMA** (Romagnesi) Noordeloos (1983). Epicutis hymeniform or palisadic; pileus often rivulose-cracked in age; smooth, velutinous; clamp connections present. (Romagnesi).

*Type species: Rhodophyllus callidermus* Romagnesi.

Aside from the type species, some other species (tropical) indicated. But three species referred here by Horak (1983) are clampless. So is *E. incanum* (Fr.) Hesler.\*

Sect. 20. **LAETA** (Romagnesi) Sing. (*Rhodophyllus* sect. *Laeti* Romagn. *Bull. Soc. Linn. Lyon* 49: 329. 1974). Epicutis neither hymeniform nor palisadic; pileus pale or bright colored, often red; hyphae clamped; pigments intracellular. Spores cubis.

*Type species: Rhodophyllus rhodellus* Romagn. (= *Entoloma kamerunense* (Bres.) Horak).

*E. kamerunense* (Bres.) Horak; *E. lycopersicum* Horak & Sing.

Sect. 21. **PSITTACINA** (Romagn.) Sing. (= *Rhodophyllus*, sect. *Psittacini* Romagn. ex Romagn. *Bull. Soc. Linn. Lyon* 49: 329. 1974). Differs from sect. 20 in (red?), blue to blue-green pigments, present in pileus, lamellae and stipe, the latter longitudinally fibrous-striate; habit of *Hygrocybe* sect. *Hygrocybe*.

*Type species: Rhodophyllus holocyaneus* Romagn. (*Entoloma virescens* (Berk. & Curt.) Horak).

*E. virescens* (Berk. & Curt.) Horak; *E. azureoviride* Horak & Sing.; also several other (tropical) species unknown to this author; obviously also *E. hochstetteri* (Reichardt) Stevenson.

Sect. 22. **PHLEBOPHORA** Noordeloos (1983). Habit pluteoid; pileus radially venose or venulose; epicutis a trichodermium of broadly fusoid cells; pigment intracellular, sometimes in addition minutely incrusting, [brown, olive etc.]; cheilocystidia large; clamp connections present. Mostly temperate, few tropical species.

*Type species: Entoloma kittsii* Noordeloos.

Aside from the type species, three other species known (Noordeloos).

Sect. 23 (?Rigiduli, Romagn.). Differs from sect. 20 in brown pigments; these intracellular; clamp connections present. Here *E. dragonosporum* (Sing.) and probably *E. pinnum* (Romagn.) Dennis; perhaps also some other tropical (African) species, and several American species: *E. hesleri* Horak (E. gracile Hesler); *E. spadix* Hesler non sensu Horak\*\*; *E. fraternus* (Sing.) Sing. (*Rhodophyllus fraternus* Sing., *Sydotia*, Beih. 7: 97. 1973).

Subgenus VII. **Alboleptonia** (Largent & Benedict) Noordeloos (1979). Habit collybioid or omphalioïd, rarely with excentric stipe; pileus always pale, white, pinkish or with slight grey or brown tinges; pileipellis a trichoderm of interwoven hyphal

\*These clampless species may well be referable to an additional section, *Viridicaules* Largent 1974 unless, as implied by Noordeloos, to *Paludocybe*.

\*\*A specimen exactly corresponding to Hesler's type description is not *E. fraternus*.

tips, with pigment intracellular if present, clamp connections usually present. (Noordeloos\*).

*Type species: E. sericellum* (Bull. ex Fr.) Kummer.

Sect. 24. *CANDIDI* (Romagn.) Noordeloos (*Rhodophyllus* sect. *Candidi* Romagn. *Bull. Soc. Linn. Lyon* 43: 328. 1974). Same characters and same type species as the subgenus.

*E. sericellum* (Bull. ex Fr.) Kummer; also *E. albellum* (Romagn.) Sing.\*\*, *E. cyathiforme* Dennis; *E. hololeucum* (Sing.) Horak (and sensu Horak?). (See *Mycologia* 62 440. 1970).

Subgenus VIII. *Leptonia* (Fr.) Noordeloos (1981). Habit collybioid, rarely omphalioid; pileus convex with depressed or umbilicate center, rarely papillate, opaque or translucently striate when moist, not or only very slightly hygrophanous, with fibrillose to squamulose surface; pileipellis a trichoderm, hymeniform or pallisade; pigment intracellular. (Noordeloos).

*Type species: Agaricus euchrous* Pers. ex Fr.

Sect. 25. *LAMPROPODES* (Kühner & Romagnesi ex Romagnesi 1974). Habit collybioid, rarely more or less mycenoid or tricholomatoid; pileus rarely depressed, never umbilicate, frequently with bluish tinges; epicutis a cutis or a trichodermium made up of bundles of repent or slightly ascending, cylindrical, multiseptate hyphae; clamp-connections present; cheilocystidia, if present, more or less clavate.

*Type species: Rhodophyllus lampropus* (Fr.) Hesler (sensu Romagn.).

*E. euchroum* (Fr.) Donk; *E. placidum* (Fr. ex Fr.) Noodeloos; *E. lampropus* (Fr.) Hesler (sensu Kühner & Romagnesi, non Orton nec Hesler) and several other species including *E. pumanquense* (Sing.) Horak and probably *E. portentosum* Horak.

Sect. 26. *GRISEORUBIDA* (Romagn.) Noordeloos (1981). Differs from the preceding section in centrally depressed pileus and fusiform or lageniform cheilocystidia (according to Noordeloos).

*Type species: Rhodophyllus griseorubidus* Kühn.

*E. griseorubidum* (Kühn.); according to Noordeloos also *E. cocles* (Fr.) Noordeloos.

Sect. 27. *PALUDOCYBE* (Largent) Noordeloos (1981). Habitat typically collybioid, rarely omphalioid; pileus convex to broadly convex with depressed to umbilicate, usually tomentose or squamulose centre, towards margin adpressed fibrillose or almost smooth; pileipellis usually a well-developed trichoderm, hymenoderm or

\*There is a contradiction in Noordeloos's papers (1981: 3) regarding *E. roseum* (Longyear) Moser which is implied (p. 146, 1981) to have always clamp connections but is described (p. 35, 1983) with "clamp connections absent". If the type (as Hesler indicates) has clamp connections, the European species might be different.

\*\*c.n. (*Rhodophyllus albellus* Romagn., *Prodr. Myc. Madag. II. Les Rhodophylles*, p. 153. 1941).

pallissadoderm; clamp-connections absent; cheilocystidia, if present, never very much different from the basiodioles, sometimes with intracellular pigment. (Noordeloos).

Type species: *Leptonia lampropodus* sensu Orton.

*Entoloma sodale* (Kühn. & Romagn.) Horak; *E. lacteonigrum* (Sing.) Horak; *E. nubigenum* (Sing.) Sing. (*Rhodophyllus nubigenus* Sing., *Nov. Hedw.* Beih. 29: 348. 1969); *E. underwoodii* Dennis. - Also numerous other species (see Largent 1977), p. 129-273 (for species of the Pacific Coast of the United States), including *E. austroanatinum* (Sing.) Horak var. *defibulatum* (Sing.), *E. catalaunicum* (Sing.) Noordeloos; possibly *E. farlowii* (Sing.) Hesler (yellow, without trichodermium) which may, however, be referable to subgenus X, and *E. impedidum* Horak; *E. subcaelestinum* (Sing. in Freindling) Sing. (*Nolanea subcaelestina* Sing., *Izv. Kar.-Finsk. fil. Akad. N. SSSR.* 4: 84-98. 1949) and *E. incanum* (Fr.) Hesler.

Subgen. IX. **Claudopus** (W.G. Smith) Noordeloos (1981\*). Habit pleurotoid, omphaloid, or [rarely] clitocyboid; [if clitocyboid, differing from section 5 in thin (to 4 mm), pigmented stipe]; stipe central or eccentric, sometimes absent; lamellae often decurrent; pigment exclusively incrusting. (Noordeloos).

Type species: *Agaricus byssisedus* Pers. ex Fr.

Sect. 28. *UNDATI* Romagn. (1974). Characters of the subgenus.

Type species: *Rhodophyllus undatus* (Fr.) Quél.

*E. undatum* (Fr.) Moser; *E. rusticoides* (Gillet) Noordeloos; *E. blandfordii* (Henn.) Sing.\*\*; *E. depluens* (Batsch ex Fr.) Hesler; *E. byssisedum* (Pers. ex Fr.) Donk; *E. lazulinellum* (Sing.) Horak; *E. cyaneum* (Murr.) Hesler.

Note: The only other section containing pleurotoid species is sect. 30 which differs in the absence of incrusting pigment. In the blue species cited above the blue pigment is intracellular but is generally accompanied by a more or less distinct incrusting pigment. Blue species are excluded from subgenus *Paraleptonia*.

Subgen. X. **Omphaliopsis** Noordeloos (1981). Habit omphaloid, collybioid or mycenoid; pileus sometimes slightly hygrophanous, usually not; pileipellis a cutis or trichoderm made up of wide, often inflated hyphae; pigment intracellular, sometimes in addition slightly incrusting pigment on the narrow hyphae of upper pileitrama; clamp-connections present (in extra-European taxa sometimes absent); spores with dihedral base. (Noordeloos).

Type species: *Entoloma leptopipes* (Kühn. & Romagn.) Moser.

Sect. 29. *TRIGONOPHYLLI*\*\*\* Romagn. (1974). Characters as in the subgenus.

\*The basionym often indicated as "Gillet" should be W.G. Smith's, see foot note on p. 706. Fries's use of *Claudopus* in 1874 is not a misapplication.

\*\*c.n. (*Eccilia blandfordii* Henn., *Hedwigia*, Beiblatt, 39: (153). 1900).

\*\*\*\*"Trichonophylli" is considered an erroneous spelling.

*Type species: Rhodophyllus parkensis* (Fr.) Quél. sensu Kühn.

*E. leptonipes* (Kühn. & Romagn.) Moser; *E. parkensis* (Fr.), at least in the sense of Kühner; also several other species, predominantly tropical ones. If pallid or white species were included, the delimitation of *Omphaliopsis* from *Alboleptonia* must be revised.

Subgen. XI. **Paraleptonia** Romagn. ex Noordeloos (1981). Habit pleurotoid or collybioid; pileus pallid [gray] or brown; spores with basal facet [heterodiametric-ovate, type III of Pegler & Young]; clamp connections present or absent. (Noordeloos). [Pigments not incrusting, never blue].

*Type species: Rhodophyllus cancrinus* (Fr.) Quél.\*

Sect. 30. **PARALEPTONIA** Noordeloos (1981). Characters of the subgenus, but never dark brown.

*Type species: Entoloma cancrinum* (Fr.) Noordeloos (Rhodophyllus, Quélet).

*E. cancrinum* (Fr.) Noordeloos; *E. cantharelloides* (Sing.) Horak; *E. arachnoides* (Berk. & Curt.) Sing. \*\*, *E. argentinum* (Speg.) Horak; *E. porpoarachnoides* (Sing.) Sing.\*\*\*

Sect. 31. **SARCITA** (Romagn.) Noordeloos (1981). Pileus and stipe dark brown [or dark gray].

*Type species: E. sarcitum* (Fr.) Noordeloos.

*E. sarcitum* (Fr.) Noordeloos; *E. lowyi* (Sing.) Horak.

### Subordo BOLETINEAE Rea

*Brit. Basidiomycetae*, p. 5. 1922.

Syn.: *Strobilomycetinae* Gilbert, *Les Boletes*, p. 83. 1931.

**Characters:** as given in key, p. 159.

**Type genus:** *Boletus* (Boletaceae).

### KEY TO THE FAMILIES

- A. Hymenophore lamellate; lamellae usually distinctly decurrent or habit pleurotoid.
- B. Spore print never deep gray, deep olive gray, or almost blackish when fresh, but whitish, yellowish white, chamois, or brown, rarely porphyry brown to violet brown or olive; forming obligatory ectomycorrhiza with frondose trees (not *Gymnospermae*), or else facultative or no mycorrhiza; veil, if present, not glutinous; cystidia present or absent; hyphae with or without clamp connections; carpophores gymnocarpous or primarily or secondarily angiocarpous, sometimes luminescent; spores smooth or ornamented, often short, more rarely elongated, hymenophoral trama bilateral to almost regular; habit not always clitocyboid.

\* The first indication of a lectotype was Singer (1951): *R. sarcitus*; but this was proposed when *Paraleptonia* was still a nomen nudum.

\*\* c.n. (*Marasmius arachnoides* Berk. & Curt., *Journ. Linn. Soc., Bot.* 10: 299. 1869).

\*\*\* c.n. (*Rhodophyllus porpoarachnoides* Sing., *Nova Hedw.* 29: 76. 1977).

- C. Clamp connections present or absent; cystidia present or absent; hymenophoral trama variable, but not of the *Boletus*-subtype; spore print porphyry or violet brown only if lamellae close and clamp connections present; spore print never olive and spores never longitudinally winged but either smooth or uneven or spinose to verrucose; projecting cystidia absent if hyphae clampless. **PAXILLACEAE**, p. 729
- C. Clamp connections present or absent, if present - spores longitudinally winged, if absent lamellae distant and often in part transformed into spores and context blackening and spores smooth (see "A" below: *Phylloporus*, *Phyllobolellus*).  
 B. Spore print deep gray, deep olive gray, or almost blackish, rarely more greenish; forming obligatory ectomycorrhiza with conifers exclusively; veil sometimes glutinous; cystidia always present, conspicuous, projecting; habit clitocyboid (appearance somewhat of *Hygrophorus*). **GOMPHIDIACEAE**, p. 732
- A. Hymenophore mostly tubulose; if lamellate, spores with longitudinal wings or smooth (and then context blackening or, if not, bluing with ammonia on the surfaces). **BOLETACEAE**, p. 737

## **PAXILLACEAE R. Maire apud Maire, Dumée & Lutz**

*Bull. Soc. Bot. Fr.* 48: ccxlili. 1901 ex Maire, *Recherches*, p. 165. 1902 (Paxillacées); Lotsy, *Vorträge*, p. 716. 1907.

*Type genus: Paxillus* Fr.

Syn.: *Hgrophoropsidaceae* Kühn., *Bull. Soc. Linn. Lyon* 49: 414 [900]. 1980.

*Omphalotaceae* Bresinsky in Kämmerer, Besl & Bresinsky, *System & Evol.* 150: 103. 1985.

**Characters:** Pileus subtomentost to tomentose, sometimes viscid, small to large, the margin initially involute; hymenophore lamellose but the lamellae frequently connected by anastomosing veins and ridges, or the sides of the lamellae venose-rugose, more rarely the anastomoses broad and numerous and the hymenophore resembling that of *Merulius*, or else lamellae not intervenose but repeatedly forked; lamellae usually rather narrow, brownish, light tan, yellow, or orange, decurrent if a stipe is present; spore print from nearly white to "chamois" (Ridgway) or "oak" even "Coffee" or between "Alamo" and "Cocoa" or "desert" to between "desert" and "bamboo" or near "terrapin" to "cochin" and then in thick layer "Cordova" to "Chutney" or pl. 6-I-11 (Maerz & Paul); or light cream (between Ib and IIa, Romagnesi); spores small to voluminous, smooth or echinate, or verruculose, or coarsely seriatly warty-rough or with short ridges, globose, ovoid, ellipsoid, or ellipsoid-oblong, generally cyanophilic, pseudoamyloid or inamyloid; cystidia present in some species of *Paxillus*, pseudocystidia in *Phyllobolites*; hymenophoral trama ± bilateral or at least lateral stratum different from mediostratum, often almost regular even in young carpophores and bilateral only in primordia; stipe present or absent, if present - central, eccentric or lateral, without pseudorrhiza; hyphae with clamp connections, but in one section of *Paxillus* without clamp connections, with inamyloid walls, often subgelatinous in the trama of the pileus and/or hymenophore and context often soft as in boletes; the carpophores luminescent in *Omphalotus* and *Lampteromyces*. Pigments of the carpophore and/or mycelium identical or related to these of the Boletaceae (variegatic acid and derivatives); poisonous substances often present. Chemical reagents such as iron compounds, KOH, HN<sub>4</sub>OH, etc. often provoking strong color reactions. On wood and on earth, often forming ectomycorrhiza, but never obligatorily ectomycorrhizal with conifers.

**Limits:** The Paxillaceae are closely related to the Boletaceae and often difficult to distinguish from the Tricholomataceae except by chemical characters. But the affinity of the genera belonging here is convincing. The identification of the genera should not be difficult even without chemical analysis if the keys are used carefully. Among the Boletaceae, the Gyrodontoideae are closest to the Paxillaceae but differ in structure (hymenophoral never of the *Boletus*-type in the Paxillaceae) and the olive or violet tinge in the fresh spore print. Bluing hymenophore and context as well as bluing pileus surface with ammonia vapors does not occur in the Paxillaceae.

Other agarics with repeatedly forked lamellae and fleshy consistency are obviously unrelated to paxillaceous genera. Most of them e. gr. *Russula cyanoxantha*, *Leucopaxillus cerealis*, and the species of *Cantharellula* are chemically quite different having amyloid spores and no pigments of pulvinic or the variegatic-acid type. The Cantharellaceae differ strongly from the Paxillaceae in stichic basidia. The veil and the ixocutis of the pileus remove *Phyllobolites* from the Gomphaceae.

The gastromycetaceous affinities of the Paxillaceae are likewise different from those of other families since they are obviously to be found in such genera as *Austrogaster*, *Singeromyces* etc.

#### KEY TO THE GENERA

- A. Spores (light microscope) smooth; habit clitocyboid or pleurotoid.
  - B. Spore print white to cream, yellowish white.
    - C. Spores often subglobose or globose; carpophores luminescent; stipe either long and central to subcentral or short and veiled; growing cespitously or fascicularly on wood of Angiosperm trees; poisonous.
      - D. Spores small (less than 10  $\mu\text{m}$ ); veil none. 194. *Omphalotus*, p. 722
      - D. Spores very voluminous; veil distinct. 193. *Lampteromyces*, p. 721
    - C. Spores mostly ellipsoid; carpophores not luminescent; growing in small groups on earth, humus, débris, or rotten wood of various types; spores if globose, strongly pseudoamyloid; hyphae of the trama tending to be subgelatinous in many species (if spores more than 10  $\mu\text{m}$  long, see *Cantharocybe*, p. 732).
      - E. Spore print white to yellowish white; if pleurotoid - growing on angiosperm wood; lamellae forked, often repeatedly forked, not only near stipe; otherwise carpophores clitocyboid. 195. *Hygrophoropsis*, p. 724
      - E. Spore print about "chamois" (Ridgway); hymenophoral trama bilateral; pleurotoid and growing on coniferous wood; lamellae less forked, rather anastomosing or laterally corrugated (see "B" below).
    - B. Spore print from pale to deep brown, rarely porphyry brown, on drying often ferruginous (or when fresh deep olive).
      - G. Spore print deep olive, brownish olive (see Boletaceae).
        - G. Spores even when quite fresh without an olive shade.
          - H. Hyphae with clamp connections or spore print neither porphyry nor violet brown; if spore print prophyry or violet brown, lamellae close. 196. *Paxillus*, p. 726
          - H. Hyphae without clamp connections; lamellae medium distant to distant, blackening when touched (see Boletaceae).
      - A. Spores distinctly ornamented; habit clitocyboid or almost omphaloid.
        - I. Stipe narrowly annulate; pseudocystidia present; spores fusoid or fusoid-ovoid, longitudinally rugose by rows of coarse warts and short ridges. 197. *Phyllobolites*, p. 728
        - I. Stipe exannulate, veil, if present, weak or indistinct; pseudocystidia none; spores globose or subglobose, echinulate or verruculose.

- J. Spores 7.2-10  $\mu\text{m}$  in diameter; lamellae mostly anastomosing at least near stipe; epicutis a continuous trichodermial palisade; veil none; tropical and subtropical species with the appearance of a small *Paxillus*. 198. *Neopaxillus*, p. 729
- J. Spores smaller; lamellae mostly not anastomosing; epicutis, if partially trichodermial or hymeniform, not continuously so; veil mostly cortinoid, but weak and not leaving traces on the mature stipe except often an applicate silky covering; temperate and subtropical species with the appearance of a small *Clitocybe*. 199. *Ripartites*, p. 730

### 193. LAMPTEROMYCES Sing.

*Mycologia* 39: 79. 1947.

*Type species: Lampteromyces japonicus* (Kawamura) Sing.

*Characters* Carpophores distinctly pigmented, rather bright colored on the pileus, pleurotoid, luminescent (Pl. 8); pileus not viscid, not hygrophanous, fibrillose; lamellae deeply decurrent; basidia without carminophilous granulation; spore print cream (between Ib and IIa, Romagnesi); spores hyaline, smooth, inamyloid, often thick-walled, globose, very large; cystidia indistinct or none; hymenophoral trama regular, consisting of somewhat flexuous or straight, not strongly interwoven hyphae; subhymenium narrow; stipe eccentric or lateral, firm-tough, annulate from a persistent veil that consists of filamentous hyphae; context consisting of inamyloid hyphae with clamp connections. On wood.

*Development of the carpophores:* Unknown.

*Area:* Japan, probably also south to Malaya and Borneo.

*Limits:* This genus is clearly delimited from all other genera. It is related to *Omphalotus* but differs in habit and veil.

Even before the study of the chemical constitution of the pigments of *Lampteromyces* was completed, it became obvious that *Lampteromyces* is sufficiently related to *Omphalotus* to be placed in the same family as the latter. This is quite obvious when we consider "illudoids", substances chemically related to illudin, occurring in both these genera. Certainly "The uniqueness of illudin S, illudin M, illudinone and other compounds of this chemical family, coupled with agreement among other mycologists that the fungi that are known to produce these illudoids are closely related, fortifies the placement of *C. illudens*, *C. subilludens* in *Omphalotus*"\*. It places *Lampteromyces* - chemically - in the closest neighborhood of *Omphalotus*. Recently (Kämmerer et al. 1985) demonstrated atrotomentin, atrotomentinic acid, thelephoric acid and gyroporin in the mycelium of *L. japonicus*.

*State of knowledge:* My recent study of fresh specimens of the type species in Japan confirms the original diagnosis of *Lampteromyces* except for the color of the spore print which is not as indicated in the literature "white or slightly tinged lilac" (Imai) or "whitish-drab" but a light cream.

*Practical importance:* *L. japonicus* is an important poisonous species which has caused serious poisonings in Japan. It contains a toxic substance, lunamycin

\*Nair, Carey & Rogerson, *Mycologia* 75: 920-922. 1983.

(C<sub>15</sub>H<sub>22</sub>O<sub>4</sub>) according to H. Shirahama (1962). This substance is said to be cancerostatic. The illudin S was isolated by Tada et al. (1964) and is identical with lunamycin.

## SPECIES

*L. japonicus* (Kawamura) Sing. (*Pleurotus*, Kawamura; *Armillaria*, Imai); apparently also *Pleurotus olivascens* Corner and *P. decipiens* Corner.

### 194. OMPHALOTUS Fayod

*Ann. Sc. Nat. Bot.* VII. 9: 338. 1889.

*Type species:* *Pleurotus olearius* (D.C. ex Fr.) Gillet.

*Syn.:* *Monadelphus* Earle, *Bull. N. Y. Bot. Gard.* 5: 432. 1909.

*Characters:* Carpophores intermediate between pleurotoid and clitocyboid in habit; pileus fleshy, non-hygrophanous; hymenophore lamellate, luminescent when fresh, bright colored as the whole carpophore; not developing cyanic acid; spore print pure white; old spores with slightly thickened walls, subglobose to short ellipsoid hyaline, cyanophilic; lamellae deeply decurrent; basidia normal but some one-spored, and some transitions between these (sterigma not discharging a spore; pseudoparaphysoid) and the cystidioles that are often numerous near the edge of the lamellae, can be observed in certain specimens; the single sterigma of the pseudoparaphyses may even attain enormous size and finally separate from the pseudoparaphysis and float around in the preparations (binucleate conidium?); spores, basidia and hyphae inamyloid; hyphae with clamp connections, epicutis little differentiated; hymenophoral trama irregular to subregular with recognizable axillar trend (near the thin subhymenial layer); stipe fibrous, fleshy, central or eccentric; odor of *Collybia dryophila*; on decaying wood (stumps and trunks) of both coniferous and frondose trees, usually fruiting in large number; binucleate mycelium in culture non-luminescent, producing oidia (observed by Hanna and the author), and amyloid elements, containing aside from thelephoric acid also atramentin, atromentinic acid, xeromic and variegatic acid and gyroporin (Bresinsky & Best, *Sydowia*, Beiheft 8: 98-109. 1970).

*Development of the carpophores:* Unknown.

*Area:* Almost cosmopolitan but absent in Antarctica and other regions without forest trees, also absent in boreal and alpine areas.

*Limits:*

*Development of the carpophores:* Unknown.

*Area:* Probably almost cosmopolitan but not represented in boreal and alpine floras.

*Limits:* This genus has been combined with *Pholiota* subgenus *Flammula*, with *Clitocybe* and *Pleurotus* was proposed with the intention of emending the diagnoses

of these genera in order to include *Omphalotus*. However, *Omphalotus* has so many characteristic features it appears impossible to incorporate it in *Clitocybe* where it would be so isolated that a new subgenus would have to be established for it. Neither from an anatomical-morphological nor from an ecological-chemical point of view, can, in the author's opinion, identity with the genus *Clitocybe* in the classical sense or in the emended sense be claimed. The author has (1943) tentatively put *Omphalotus* in *Armillariella*, however, under the condition that the hyphae of the carpophore are clampless. Further studies, however, have shown that clamp connections are constantly present. Its identification with *Pleurotus* cannot be admitted under present circumstances considering the much narrower sense in which *Pleurotus* is now conceived. The species left in *Pleurotus* are absolutely not allied to *Omphalotus* from whatever point of view they are examined, unless the substratum is made the decisive factor. The spores are short in *Omphalotus*, and cylindric in *Pleurotus*. The hymenophoral trama is much more irregular (to almost intermixed) in *Pleurotus* than in *Omphalotus*. The subhymenium is much more distinct from the trama and forms a broader layer in *Pleurotus* than in *Omphalotus*; the spore print is livid inmost monomitic species of *Pleurotus*, and the stipes are, in an aereage, more eccentric in *Pleurotus*. The genus *Omphalotus* does not seem to be related to *Gerronema*, a genus which, in some of its species, has the yellow pigments, wood-inhabiting mycelium, and claps as well as occasionally elements transitional between one-spored basidia and cystidioles but differs in habit and chemical characters.

The chemical characters have been most important in the acceptance of the suggestion formulated by Bresinsky (1974) to revise the position of *Omphalotus* in the Tricholomataceae. These chemical characters - first mentioned by Singh & Anchel (*Phytochemistry* 10: 3259. 1971, for atromentic acid) explain, in a sense, the taxonomical isolation of *Omphalotus* (and *Lampteromyces*) in the Tricholomataceae. The pigments alone would have made a transfer to the Paxillaceae, if probable, yet, still not fully conclusive (cf. Singer, *Persoonia* 11, 1981, p. 273, 295, 296) but the similarity of the characters exhibited by *Omphalotus* on one hand and *Hygrophoropsis* on the other (cf. Kühner 1977) have convinced both Moser (1978, 1983) and myself that *Omphalotus* is best classified among the Paxillaceae. Corner (1981) is the only modern author who returns to Gillet, disregarding the chemotaxonomy and inserting *Omphalotus* (and *Lampteromyces*) as mere synonyms of *Pleurotus*.

*State of knowledge:* Six species have been described which belong here, but see below.

*Practical importance:* *Omphaloti* are active destroyers of timber; besides they are poisonous (containing illudin S), thus, in spite of their beauty rather undesirable in the forests. It is possible that the yellow pigment can be extracted and used for stains in cytological laboratories. The American race or species (*illudens*) contains two antibiotica (illudin M and illudin S), and the subilludens-race or species contains lysergic acid derivatives both in the carpophore and the mycelium; but this report is in need of verification (Tyler 1965).

## SPECIES

*O. olearius* (D.C. ex Fr.) Sing. [Pleurotus, Gillet; Clitocybe, R. Maire; Flammula phosphorea (Batt. ex Quél); *O. olivascens* Bigelow; also *Clitocybe illudens* (Schwein.) Sacc., *Panus incandescens* Berk. & Br., *Pleurotus facifer* (Berk. & Curt.) Sacc., and *Monadelphus subilludens* Murr. - Whether the latter five species are geographical races (subspecies) or microspecies worthy of transference to *Omphalotus* (where necessary) can be decided only by experimental methods (compatibility or incompatibility of monosporic cultures).

### 195. HYGROPHOROPSIS (Schröt. in Cohn) R. Maire apud Martin-Sans

*L'Empoisonnement*, p. 99. 1921.

*Type species: H. aurantiaca* (Wulfen ex Fr.) R. Maire.

*Syn.: Cantharellus* subgenus *Hygrophoropsis* Schröter apud Cohn, *Krypt.-Fl. Schlesien, Pilze* 1: 511. 1889.

*Merulius* S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 636. 1821 (non Fr.).

*Characters:* Pileus somewhat tomentose with involute margin when young; spore print white to yellowish white or pale cream; hymenophore lamellate; lamellae decurrent, narrow, arcuate, with somewhat obtuse edges and strongly, usually repeatedly forked, sometimes anastomosing; spores subhyaline or with a yellowish reflex, smooth, small to barely mediumsized, with thin, simple, inamyloid or pseudoamyloid, always cyanophilic walls, subglobose, short-ellipsoid, ellipsoid, ellipsoid-oblong, or cylindric; basidia small and mostly 4-spored, normal in all regards; cystidia absent; hymenophoral trama at first mostly (often vaguely) bilateral, soon becoming subregular, mediostratum of interwoven, often firm- to thick-walled, rather broad hyphae, tapering and often not reaching the edge, the lateral stratum consisting of narrower, generally thin-walled hyphae and here frequently looser and subgelatinous, the hyphae in mature specimens mostly running in several directions, connecting with the narrow to broad subhymenium consisting of multiseptate hyphae (sometimes an indistinct hymenopodium differentiated between it and the lateral stratum); stipe fleshy, if present, but varying between central, eccentric, lateral and absent, without any traces of veil; context fleshy-soft as in the Boletoidae; chemical color reactions with FeSO<sub>4</sub>, KOH and HN<sub>4</sub>OH not striking; xerocomic acid absent in carpophore; variegatic acid, varigotorubin, xerocomic acid, demonstrable in mycelial cultures. On the ground, in deep moss, and on wood or sawdust, not obligatorily ectomycorrhizal.

*Development of the carpophores:* Gymnocarpous; stipiticarpous (in the type species).

*Area:* In the temperate, subtropical and tropical zones of both Hemispheres.

*Limits:* The non-luminescence of all carpophore parts and the shape of the spores differentiate this genus from the two preceding ones. As for *Paxillus*, it could only be confused with *Paxillus* sect. *Panuoides* where the spore print is differently

(although pale) colored and the pleurotoid carpophores develop only on coniferous hosts. *Hygrophoropsis* differs from *Clitocybe* in the pigments observed in the mycelium, the frequently pseudoamyloid and always cyanophilic spores, the softer fleshy context of pileus and stipe and the forking of the lamellae (which occurs in *Clitocybe* only exceptionally).

After having redefined this genus and inserted it in the Paxillaceae, I at first admitted only species with pseudoamyloid spores, as have many Paxillaceae. These species were *H. aurantiaca* and *H. tapinia* (its identity with *Cantharellus flabelliformis* Berk. & Curt. cannot be accepted since the type has no spores and its description does not fit *H. tapinia!*). Only in 1975 I have added some species with inamyloid but cyanophilous spores. These species, with regard to their other characters, coincide with the type species. The spore wall of the latter was here described as simple not 'thin-walled' and not 'mince et simple' as Kühner quotes me) and in my description of *H. aurantiaca* (Singer 1946, see Singer, 1977a) was described as simple not 'thin-walled' (and not 'mince et simple' as Kühner quotes me) and in my description of *H. aurantiaca* (Singer 1946, reprint 1977) was de- the endosporium not very thick but well characterized. This, according to him, is not the case in *H. olida* although the spores, as indicated by me, are cyanophilous as in *H. aurantiaca*. I have also observed rather thickish wall in *H. kivuensis* Heinemann (Singer et al. 1981) and we have weakly to strongly pseudoamyloid spores together with inamyloid spores in *H. panamensis*. Consequently there is a continuity of spore characters if extra-European species are considered. On the other hand, *Gerronema albidum* which differs not only by acyanophilous spores but by absence of clamp connections (in contrast to all *Hygrophoropsis* species), cannot be placed at the end of this series inasmuch as chemotaxonomy cannot be of much help here since *G. albidum* carpophores are almost pigmentless; however, a pigment analysis of the closely related *G. alutaceum* and E.M. sections of their spores may possibly add some further evidence in the case. For the time being, the hiatus appears to be between *H. olida* and *G. albidum*, not between *G. albidum* and the rest of the *Gerronemas*, and the circumscription of *Hygrophoropsis* must remain the same (Singer 1975; Pegler & Young 1981).

As for *Cantharocybe*, see under that genus, p. 732.

*State of knowledge:* Six species are now known in all essential details and belong with certainty in *Hygrophoropsis*.

*Practical importance:* *H. aurantiaca* was formerly believed to be poisonous but its edibility after boiling is now established. Like *Paxillus involutus*, it may be poisonous when consumed raw. This seems to be suggested by experiments carried out in Finland by E.-L. Hintikka (*Karstenia* 18, suppl.: 40-42. 1978) who found extracts of both *H. aurantiaca* and *P. involutus* to be toxic to U cells (U-4, Orion, originating from human amnion).

## SPECIES

### 1. Species with pseudoamyloid spores:

*H. aurantiaca* (Wulff ex Fr.) R. Maire apud Martins-Sans (*Cantharellus*, Fr.; *Merulius*, Pers ex S.F. Gray; *Clitocybe*, Studer) with var. *aurantiaca* and var. *nana* Sing.; *H. fuscosquamulosa* Orton; *H. tapinia* Sing.; *H. panamensis* Sing.; obviously also *H. coacta* McNabb (but extremely close to the type species).

### 2. Species with inamyloid spores.

*H. rufescens* (Quél.) Sing.\* (*H. olida* (Quél.) Métrod; *H. morgani* (Peck) Bigelow); *H. kivuensis* Heinemann.

## 196. **PAXILLUS** Fr.

*Flor. scan.*, p. 339. 1835.

*Type species: P. involutus* (Batsch ex Fr.) Fr.

*Syn.: Ruthea* Opatowski, Comm. Bolet., *Wiegmannia* 2: 4. 1836.

*Rhymovis* Rabenh., *Kryptogamenflora* 1: 453. 1844.

*Tapinia* Karst., *Hattsv. Bidr. Finl. Nat. Folk.* 32: xxiii. 1879.

*Tapinia* (Fr. "tribus") Pat., *Hym. Eur.* p. 130. 1887.

*Tapinella* Gilbert, *Bolets*, p. 67. 1931.

*Paxillopsis* Gilbert, *Bolets*, p. 86. 1931 (nom. nud.), non Lange (1939).

*Parapaxillus* Sing. ad. int., *Ann. Mycol.* 40: 58. 1942.

*Characters:* As in *Hygrophoropsis* but spore print at least "chamois" (Ridgway) or deeper brownish (e. gr. "oak", or Pl. 14, J. 11-12 to K 11-12, Maerz & Paul); spores yellowish to brownish under the microscope, smooth, with moderately thin wall without germ pore or callus; lamellae often anastomosing, especially near the stipe, sometimes venose rugose on the sides, often easily separable from the context of the pileus; hymenophoral trama often consisting of a mediostratum, a diverging lateral stratum and an irregular hymenopodium (e. gr. in *P. involutus*), or else of simpler structure but always diverging; stipe central, eccentric, lateral, or absent; veil present, or more often absent; context sometimes becoming brown; cystidia sometimes present on the sides and edges of the lamellae; basidia normal in every regard; chemical color reactions with FeSO<sub>4</sub>, KOH, NH<sub>4</sub>OH, etc. usually striking. On the ground and on wood (Pl. 44).

*Development of the carpophores:* "Pseudoangiocarpous" in the type species, probably in all other species likewise.

*Area:* Widely distributed (like *Hygrophoropsis*), but particularly rich in forms in the temperate and tropical zones of South America (as in generally the case in this family).

\*c.n. (*Cantharellus rufescens* ("Paulet" ex) Quél. *Mem. Soc. Emul. Montbéliard* II. 5: 441. 1875).

**Limits:** The delimitation from other paxillaceous genera is easy if the characters emphasized in the keys are taken fully into consideration.

*Crepidotus* is sometimes similar, as has been pointed out by Pilát who inserts the pleurotoid forms in *Crepidotus*. There is, however, no difficulty in separating *Paxillus* from *Crepidotus* if the structure of the hymenophoral trama and the chemical characters of both genera are taken into consideration. Pseudoamyloid spores do not exist in *Crepidotus*.

**State of knowledge:** Most species of *Paxillus* are well known. They have been monographed by Singer for Florida (1946), for South America (1964). 12 species are now recognized.

**Practical importance:** *P. panuoides* is an active wood destroyer and forms carpophores even in the darkness of coal mines, cellars and similar places. In contrast to *Lentinus lepideus* these carpophores are normally developed. The timber attacked is weakened and destroyed. *P. involutus* is the "babye okhy" of the Russian farmer who considers it second rate but salts it in large quantities in years when other mushrooms are scarce. It is also eaten in some parts of Central Europe e. gr. around Berlin, but has caused poisoning in other parts of Germany and in Poland; it is now thought to be necessary to boil it well and discard the liquid before using it for the table. This fungus causes acute insufficiency of the kidney due to hemolytic anemia (see Schmid, Hartmann, Würstlin & Deicher, *Deutsche Mediz. Wochenschr.* 96: 1188-1191. 1971). Stadelmann et al. (*Helvet. Chim. Acta* 59: 2434. 1976) have found significant amounts of epimuscarin in *P. involutus* but Flammer (*Schw. Med. Woch.* 113: 1555-1561, 1983) considers the "Paxillus-syndrome" as allergic. *P. atrotomentosus* causes brown root rot in dead *Pinus banksiana* according to R.N. Davidson & R.F. Patton (1961). While *P. involutus* is facultatively ectomycorrhizal (and therefore important in the succession of forest communities), some species of the south-temperate (*Nothofagus*-)zone, such as *P. boletinoides* and *P. defibulatus* are obligatorily ectomycorrhizal. The latter is used as food and sold in the markets both dried and fresh in Southern Argentina and Chile.

## SPECIES

Sect. 1. *PARAPAXILLUS* (Sing.) Sing. Clamp connections present; veil present.

**Type species:** *P. argentinus* Speg.

*P. argentinus* Speg.; *P. boletinoides* Sing.

Sect. 2. *ATROTOMENTOSI* Sing. (1946). Stipe present, vellereous, central or eccentric, more rarely lateral; veil none; spores small (up to 7.5  $\mu\text{m}$  long); cystidia none.

**Type species:** *P. atrotomentosus* (Batsch ex Fr.) Fr.

*P. atrotomentosus* (Batsch ex Fr.) Fr.; *P. guttatus* Sing.; *P. polychrous* Sing.; perhaps also *P. pahangensis* Corner.

Sect. 3. *PANUOIDES* Sing. (1946). Pileus almost sessile; spores sometimes pseudo-

amyloid (in *P. panuoides* and *P. serbicus*), small (up to 6  $\mu\text{m}$  long); cystidia none; veil none.

*Type species:* *P. panuoides* (Fr. ex Fr.) Fr.

*P. panuoides* (Fr. ex Fr.) Fr. (*P. rufus* Berk. & Curt.; *P. ligneus* Berk. & Curt.; *P. acheruntius* (Humb. ex) Schröt.; *P. lamellirugis* Quél.; *Agaricus scobigenus* Pers.; *A. bubalinus* Pers.; *Cantharellus crucibulum* (Fr. ex Pers.) Fr.; *Leptotus*, Karst. (with f. *ionipus* (Quél.) Joss.); *P. serbicus* (Pilát) Sing. (*Crepidotus*, Pilát); *P. curtisii* Berk. apud. Berk. & Curt. (*P. corrugatus* Atk.); probably also *Merulius agathidis* Corner.

Sect. 4. *PAXILLUS*. (Involuti Sing. 1946). Pileus centrally, eccentrically, or more rarely laterally stipitate; stipe glabrous; veil none; spores larger than 6  $\mu\text{m}$ ; (pleuro-) cystidia present; clamp connections present.

*Type species:* *P. involutus* (Batsch ex Fr.) Fr.

*P. involutus* (Batsch ex Fr.) Fr.; *P. vernalis* Watling (*P. vernalis* Smith & Sing. 1962 ined.); *P. rubicundulus* Orton (often erroneously called *P. filamentosus* Fr. or *P. leptopus* Fr.\*).

Sect. 5. *VELUTICIPITES* Sing. (1961). Differs from the preceding section in the absence of cystidia and mostly larger spores (13-26  $\mu\text{m}$  long or, according to McNabb, in one species only 7.8-11  $\times$  4.5-5.8-(6.8)  $\mu\text{m}$ ). Species of the Southern hemisphere.

*Type species:* *P. veluticeps* (Cooke & Mass.) Sing.

*P. veluticeps* (Cooke & Mass.) Sing. (*Crepidotus pactolus* Cooke ex Pilát; *Paxillus infundibuliformis* Cleland); according to McNabb also *P. nothofagi* McNabb; possibly also *Flammula statuum* Speg. (cf. Singer, *Nov. Hedw.* 7: 113, 1964).

Sect. 6. *DEFIBULATI* Sing. (1961). Carpophores without veil, without clamp connections.

*Type species:* *P. defibulatus* Sing.

*P. defibulatus* Sing.; obviously also *P. aurantiacus* McNabb and *P. squarrosum* McNabb; also *P. muelleri* Berk. (as for the type see Singer, *Nov. Hedw.* 7: 113. 1964; Pegler, *Austr. J. Bot.* 13: 340. 1965; Horak, *Austr. Journ. Bot. Suppl. Ser.* 10: 5. 1983).

## 197. **PHYLLOBOLITES** Sing.

*Ann. Myc.* 40: 59. 1942.

*Type species:* *Phyllobolites miniatus* (Rick) Sing.

\**P. leptopus* Fr. is merely a pleurotoid, non-ectotrophic form of *P. involutus*, growing on wood.

**Characters:** habit clitocyboid, reminiscent of that of *Paxillus involutus* but (in the type species) with a red pileus covered with an ixocutis; hymenophore lamellate with a few lamellae forked and with scattered intervenosity, all decurrent, rather broad, at first pallid later ocher from the spores, close or subclose; hymenophoral trama with a gelatinized mediostratum and a broad, less or scarcely gelatinized lateral stratum, consisting of hyphae and gloeo-vessels which at least near and at edge are divergent; subhymenium of multi-septate hyphae, scarcely gelatinized; basidia (2)-4-spored; pseudocystidia numerous and conspicuous, eventually somewhat coccinoid; spores fusoid, more rarely subfusoid-ovoid, with suprahilar depression or applanation, without apical pore, with firm wall which is coarsely warty from longitudinal series of verrucae and short ridges, deep ochraceous in KOH becoming more brown in Melzer but not typically pseudoamyloid, medium sized (to 12  $\mu\text{m}$  long); stipe central, solid or soon becoming hollow; veil present, forming a very narrow and somewhat fugacious, strictly apical annulus which is thin, membranous, not viscid; basal mycelium very scanty; KOH on pileus negative. On the ground in ectotrophic forests, gregarious.

**Development of the carpophores:** Unknown, but certainly not gymnocarpous.

**Area:** Tropical South America.

**Limits:** Clearly delimited from other boletineous genera.

**State of knowledge:** Only one species is known.

**Practical importance:** *P. miniatus* is apparently ectomycorrhizal.

## SPECIES

*P. miniatus* (Rick) Sing. (*Paxillus*, Rick).

### 198. NEOPAXILLUS Sing.

*Mycologia* 40: 262. 1948.

**Type species:** *N. echinosporus* Sing. (= *N. echinospermus* (Speg.) Sing.).

**Characters:** Habit clitocyboid-omphaloid, reminiscent of a small form of *Phylloporus rhodoxanthus* or *Paxillus*; pileus depressed in the center; cuticle - a trichodermium palisade consisting of brown (by an intraparietal pigment) hyphal chains which are erect and parallel with each other or subparallel, the terminal member broadly clacate (17-42 ( 5-17  $\mu\text{m}$ ); hymenophore lamellate, lamellae rather distant, occasionally anastomosing by veins, dull rusty brownish in dried specimens, deeply decurrent and anastomosing at the stipe; hymenophoral trama in youth weakly or vaguely bilateral, later consisting of a mediostratum of subparallel strictly axillary arranged hyphae, the mediostratum flanked by the interlaced-intermixed, broad lateral stratum which is little differentiated from the hymenopodium where the

hyphae are densely packed and only at places tending to be subparallel, accompanying the subhymenium around the interlamellar spaces; subhymenium - a thin layer, well developed but not very sharply delimited with regard to the subjacent hymenopodium, consisting of short-cylindric to subisodiametric cells; basidia 4-spored, some 2-spored, clavate; cystidia none in the type, but some sterile cells (cystidioles) often seen on the edge and near it; spore print near "oak" (Maerz & Paul); spores under the microscope with a rusty brown ornamentation on paler ground, the wall at first apparently homogeneous and smooth, then punctate, and at maturity beset with cylindric spines of 0.8-1.0  $\mu\text{m}$  (in the type species) whose lower portion may be somewhat inserted in the wall proper, wall moderately thick, not interrupted by a germ pore or a callus, size of the spores medium (7.2-10  $\mu\text{m}$  in diameter), shape globose; stipe central or almost so, without a veil; mycelium whitish, sparse. All hyphae with clamp connections. FeSO<sub>4</sub> olive on pileus; deeper colored with NH<sub>4</sub>OH and KOH; phenol causing a reddish chocolate discoloration. On the ground.

*Development of the carpophores:* Unknown.

*Area:* Tropical and subtropical South and Central America.

*Limits:* *Neopaxillus* is close to both *Paxillus* and *Ripartites*. It is easily distinguished from both these genera by the characters indicated in the key. *Neopaxillus* may be confused with *Melanomphalia* from which it differs in spore shape and ornamentation and the structure of the hymenophoral trama.

*State of knowledge:* Only one species is known.

*Practical importance:* *N. echinospermus* (Speg.) Sing. is apparently a component organism of the tropical cicatrizing mycorrhiza, thus facultatively ectomycorrhizal and of potential importance in tropical forestry.

## SPECIES

*N. echinospermus* (Speg.) Sing. (*Naucoria*, Speg.; *Neopaxillus echinosporus* Sing.).

### 199. RIPARTITES Karst.

*Hattsv., Bidr. Finl. Nat. Folk* 32: xxiv. 1879.

*Type species:* *R. tricholoma* (A. & S. ex Fr.) Karst.

*Characters:* Pileus whitish to rusty brown or argillaceous brown, often with appressed fibrillose squamules or with fimbriate margin, slightly to strongly sticky-viscid, depressed in age, with involute margin, subhygrophanous or nonhygrophanous; cuticle not organized into a trichodermium or a hymeniform structure, without dermatocystidia and without spherocysts; lamellae decurrent or adnate; hymenophoral trama rather regular than bilateral, consisting of somewhat to strongly interwoven hyphae but generally  $\pm$  axillary arranged filamentous elements, these near the subhymenium often a long time slightly divergent (*Clito-*

*cybe*-type); basidia small, normal, but occasionally long-pedicellate and then reaching more than 35 µm in length; cystidia absent on the sides of the lamellae but cheilocystidia mostly differentiated (although not striking); spore print between "Desert" and "Bamboo" (Maerz & Paul), under the microscope pale brown, echinulate, very small and globose, generally reminding one of the conidia of some Aspergillaceae but asymmetric (heterotropic); inamyloid, without germ pore and callus, with apparently simple wall, uninucleate, cyanophilic especially in the warts (see Pl. 47, 1, 4); stipe central or nearly so, well developed; veil present, cortinoid or thinly membranous, soon disappearing without leaving very distinct marks on the mature carpophores; all hyphae with clamp connections, inamyloid. On rotten débris in the forest, also on humus and sand and among mosses.

*Development of the carpophores:* Gymnangiocarpous, stipitocarpous.

*Area:* Temperate zone of the northern and southern hemisphere, also in the sub-tropical zone of Argentina.

*Limits:* The delimitation of this genus is not difficult, but its position has been discussed by various authors; *Ripartites* has been identified with *Paxillus* (Quélet) but has also been treated as a species of *Flammula* and *Inocybe*. It has recently been treated in the Crepidotaceae, the Tricholomataceae and the "Ocellées" (Kühner & Romagnesi) which are a small group of tricholomataceous (*Rhodopaxillus*) and rhodophyllaceous (*Clitopilus*) genera (now abandoned by Kühner). A quantitative appraisal of the whole of the available characters of *Ripartites* shows that it was Quélet who came closest to the correct solution, cf. Machol & Singer (1972, p. 771). I consider this solution correct not only because of the outcome of the numerical essay but because, on second thought, *Ripartites* is indeed very close to *Neopaxillus*, and the hilum of the spores is of the open-pore type (as in *Paxillus*) according to Pegler & Young (1971).

*State of knowledge:* The type species is known fully, including its cytology, development and distribution; all together five species are here recognized.

*Practical importance:* Unknown.

## SPECIES

*R. strigiceps* (Fr.) Karst.; *R. tricholoma* (A. & S. ex Fr.) Karst.; *R. helomorpha* (Fr.) Karst.; *R. amparae* Sing.; *R. metrodii* Huijsman (*Paxillus scambus* (Fr.) Ricken sensu Ricken non Fr.; *R. tricholoma* var. *helomorpha* (Fr.) Metrod non Fr.; *Paxillopsis helomorpha* (Fr.) Lange sensu Lange non Fr.). Moser (1967, p. 151) also refers here: *R. albidoincarnata* (Britz.) Konr. & Maubl. and *R. serotina* Einhellinger (*Omphalia pyxidata* (Bull. ex Fr.) Kummer sensu Ricken non al.) which is interpreted as *Hygroaster asterosporus* (Lange) Sing. by Orton but the description (Ricken 1: 391) favors the interpretation by Moser.

## GENERA INCOMPLETELY KNOWN

*Cantharocybe* Bigelow & Smith, *Mycologia* 65: 486. 1973. This genus is characterized by clitocyboid habit, large carpophores, long-decurrent lamellae which are anastomosing or forming a reticulum on the stipe apex, the colors yellow ("Naples yellow", "straw yellow", "primuline yellow", Ridgway), the spores smooth elliptic to oblong or subcylindric, (11-16(17.5) × (4.5)-6-7.5 µm), forming a white or pale lemon yellow spore print; hymenophoral trama of undulate-subparallel to parallel hyphae which are cylindric, with clamp connections; cheilocystidia abundant and large (37-60 ( 7-12 µm); habitat on needle bed and earth under conifers. The type (and only) species is *C. gruberi* (A.H. Smith) Bigelow & Smith. (*Clitocybe*, A.H. Smith; *Laccaria*, Sing.).

I agree now, comparing my notes on the type with Bigelow & Smith's redescription, that - although both data agree well - *C. gruberi* is not a *Laccaria*, and that it represents a good monotypic genus. If left in the Tricholomataceae, the data available would probably be sufficient to insert it in the Tricholomateae and recognize it among the well defined genera. I have now established that all species of *Laccaria* have at maturity at least a majority of finely asperulate to long-spinose spores and none of the fully described Laccarias has a yellow pigment like the one observed in all parts of *Cantharocybe*. However, the pigment and the sum of all characters known strongly suggest that *Cantharocybe* is a paxillaceous genus. On the other hand, some characters important in the latter family, have not been available (mainly a chemical identification of the pigments in the carpophore and those developed in the mycelial cultures; presence or absence of luminescent parts in the carpophore; a more precise indication of the color or color variation of the spore prints; pseudoamyoidity of sporal or hyphal walls and their behavior in cotton blue mounts; thickness or swelling of the spore walls; obligatory or facultative ectomyorrhizal association, and chemical color reactions).

If, indeed, the pigments should (as expected) at least in part be identical with those found in *Hygrophoropsis* and/or other paxillaceous genera, *Cantharocybe* should be inserted between *Omphalotus* and *Hygrophoropsis*.

## GOMPHIDIACEAE R. Maire ex Jülich

*Publ. Junta Ciénc. Nat., Barcelona*, p. 43. 1933; *High. Taxa Basid.*, p. 369. 1981.

*Type genus: Gomphidius* Fr.

*Characters:* Habit clitocyboid; pileus glabrous or tomentose or farinaceous-mealy, viscid to glutinous or more rarely dry, small to rather large; hymenophore lamellate, rarely strongly anastomosing and almost loculate, but not tubular nor boletinoid, lamellae rather thick and decidedly decurrent, frequently with obtuse edges (less so in most species of *Chroogomphus*), waxy-subgelatinous (especially in *Gomphidius*), subdistant to distant, more rarely subclose, more or less arcuate or descendant, gray to fuliginous in age but assuming a rusty fuliginous tinge when kept in herbarium

for a long time, especially in *Chroogomphus*; spore print from "bone brown" (Ridgway) to "Buffalo" (Maerz & Paul) to nearly black, rarely "elm green", "Roman green", "buffy citrine" (Miller), usually, at least in *Chroogomphus*, assuming a rusty brown color when dehydrated; spores always elongate, fusoid to subcylindric, mostly with distinct suprahilar depression, without a distinct germ pore or apical truncation or callus in most cases, smooth, melleous or grey under the microscope, cyanophilic, inamyloid or sometimes weakly pseudoamyloid; basidia normal and usually 4-spored, rather elongated when sporulating; cystidia often of the oleocystidial type and distinctly incrusted by a resinous matter of chestnut or fulvous color, sometimes with partly or almost entirely strongly thickened walls, numerous to (rarely) scattered; hymenophoral trama bilateral, the mediostratum consisting of parallel to subparallel hyphae forming a thin, sometimes evanescent layer, the lateral stratum at first consisting of diverging hyphae, often indistinct in old specimens; hymenopodium very broad, consisting of strongly interwoven and entirely irregular elements which are not clearly separated from the subhymenium in some species while in others the latter is well differentiated; subhymenium variable in structure; stipe versiform, equal or swollen, etc., in most species and specimens with a discolored (bright yellow rarely reddish to pink) base both inside and on the surface; veil present or absent, more often present, and then either entirely glutinous, or tender and fibrillose, or mealy and consisting of a loose pseudoparenchyma, sometimes forming an annulus; glandulae present on the surface of the stipe of only one species; all hyphae without clamp connections in the carpophore, rarely (according to Miller in American collections of *Gomphidius maculatus*) very scarce clamps, sometimes present in the basal mycelium, inamyloid or sometimes weakly pseudoamyloid, or with amylaceous incrustations. On earth, forming obligatory ectomycorrhiza with conifers.

#### KEY TO THE GENERA

- A. Veil consisting of spherocysts. 200. *Cystogomphus*, p. 733
- A. Veil not consisting of spherocysts only.
  - B. Context of pileus usually quite white unless reddened by autoxidation; amylaceous incrustations absent on the hyphae; gomphidic acid present. 201. *Gomphidius*, p. 734
  - B. Context of pileus not white; amylaceous incrustations present on some or all hyphae; gomphidic acid often (or always?) absent. 202. *Chroogomphus*, p. 735

#### 200. CYSTOGOMPHUS Sing.

*Ann. Mycol.* 40: 51. 1942.

*Type species:* *C. humblotii* Sing.

*Characters:* As in the family, but veil consisting of spherocysts. On the ground in coniferous plantations.

*Development of the carpophores:* Not studied in detail.

*Area:* Unknown. The type species is known only from coniferous plantations near Paris. The conifers were of foreign origin.

*Limits:* These are clearly recognizable in the key.

*State of knowledge:* This genus contains thus far only one species which is perfectly well known in all essential characters.

*Practical importance:* Probably a mycorrhizal fungus, and therefore potentially important in forestry.

## SPECIES

*C. humblotii* Sing.

### 201. **GOMPHIDIUS** Fr.

*Flor. scan.* p. 339. 1835.

*Type species:* *G. glutinosus* (Schaeff. ex Fr.) Fr.\*

*Syn.:* *Leucogomphidius* Kotl. & Pouz., Česká Myk. 26: 219. 1972.

*Characters:* Those of the family, but veil never consisting of spherocysts, but frequently gelatinized and hyphae without amylaceous incrustations, context of the pileus usually white but yellow in the base of the stipe, sometimes reddening, or red in the base of the stipe; gomphidic acid and/or atromentinic acid present.

*Development of the carpophores:* Metavelangiocarpous and stipitocarpous in *G. glutinosus* and *G. roseus* (Reijnders) and apparently so in all species.

*Area:* North-temperate zone.

*Limits:* These are clearly recognizable in the key.

*State of knowledge:* The genus has been monographed several times and its species are now well known. We admit eight species.

*Practical importance:* The *Gomphidiaceae* are specialized and obligatory ectomycorrhizal fungi and as such they are likely to play a major practical rôle in forestry, especially in reforestation projects. The association of some species of *Gomphidius* with species of *Suillus* is remarkable inasmuch as the hyphae of the corresponding pairs (like *Gomphidius roseus* - *Suillus bovinus*, *Gomphidius maculatus* - *Suillus grevillei*) are often concrescent and even the carpophores may be found concrescent at their bases. Whether this phenomenon is based on practically identical ecological requirements for vegetative development as well as for fruiting conditions and host

\*The earliest selection of a lectotype refers to *G. viscidus* which, however, as such, does not appear in the original species and consequently has been substituted by *G. glutinosus*. It should be kept in mind that *A. viscidus* Pers. quoted by Fries as synonym of *G. glutinosus* is actually this species, not *G. viscidus* (L. ex Fr.) Fr. as later substituted for *A. rutilus* by Fries (1838). See also *Taxon* 22: 445. 1973.

specialization is still an unanswered question. Possible other explanations may be seen in the incapacity of the *Gomphidii* to produce those growth substances necessary for mycorrhization of the conifer roots and dependence on the *Suilli* in this regard, or even in a parasitic relationship.

All *Gomphidii* are edible (in spite of Fries's statement "vix cibarii, subinsipidi").

## SPECIES

Subgenus I. **Laricogomphus** Sing. (1948). Context turning pink when bruised; veil (glutinous or fibrillose) inconspicuous, almost nil; dermatocystidia of the stipe fasciculate, forming small, dark glands or fibrils; spores larger than 14  $\mu\text{m}$ . Mycorrhiza with *Larix*.

Type species: *G. maculatus* (Scop. ex Fr.) Fr.

*G. maculatus* (Scop. ex Fr.) Fr. (*G. gracilis* Berk. & Br.).

Subgenus II. **Gomphidius**. (*Myxogomphus* Sing. 1948). Context of the pileus unchanging or more rarely turning pink when bruised; veil well developed, consisting of subparallel-subinterwoven hyphae which are mostly strongly gelatinized; dermatocystidia of the stipe not forming dark fibrils or glands on the stipe (unless pileus pink and spores smaller than 14  $\mu\text{m}$ ). Mycorrhiza with various conifers but only exceptionally with *Larix*.

Type species: *G. glutinosus* (Schaeff. ex Fr.) Fr.

Sect. 1. **GOMPHIDIUS** (*Macrosporus* Sing. 1948; *Roseogomphus* Miller 1972). Mature spores longer than 14  $\mu\text{m}$ .

Type species: *G. glutinosus* (Schaeff. ex Fr.) Fr.

*G. septentrionalis* Sing.; *G. nigricans* Peck; *G. smithii* Sing.; *G. roseus* (Fr.) Karst.; *G. subroseus* Kauffm.; *G. glutinosus* (Schaeff. ex Fr.) Fr.; obviously also *G. largus* O.K. Miller.

Sect. 2. **MICROSPORUS** Sing. (1948). Mature spores 14  $\mu\text{m}$  long or shorter.

Type species: *G. oregonensis* Peck.

*G. oregonensis* Peck; obviously also *G. pseudomaculatus* O.K. Miller.

### 202. **CHROOGOMPHUS** (Sing.) O.K. Miller

*Mycologia* 56: 529. 1964.

Type species: *G. rutilus* (Schaeff. ex Fr.) Lundell & Nannfeldt.

Syn.: *Gomphidius* subg. *Chroogomphus* Sing., *Pap. Mich. Acad. Sc. Arts & Lett.* 32: 150. 1946 (publ. 1948).

Characters: Those of the family, but context of the pileus  $\pm$  pigmented; hyphae all

or many with amyloseous incrustation, those of the veil usually parallel or subparallel and incrusted; subhymenium dense, filamentous-intermixed and irregular; gomphidic acid absent (in *G. helveticus*, and probably in all species), but xerocomic acid and helveticon/bovinon present (Besl et al. 1975). Pl. 75, 1-4.

*Development of the carpophores:* Metavelangiocarpous and stipitocarpous according to Reijnders, at least in the type species.

*Area:* Temperate zone of the northern hemisphere, probably all through the area of coniferous forests and with them entering the subtropical zone and the mountain regions of Central America; also outside this area introduced with conifer plantations.

*Limits:* These are evident from the keys.

*State of knowledge:* Ten species are recognized here. 20 species and subspecies have been keyed out by us (*Česká Myk.* 10: 86-88. 1976).

*Practical importance:* *C. rutilus*, *C. helveticus*, and perhaps all species are edible, all are ectomycorrhizal with conifers.

## SPECIES

Sect. 1. *FLOCCIGOMPHUS* (Imai) O.K. Miller (1964). Pileus dry to barely subviscid, not shining when dry, more or less tomentose or fibrillose; epicutis of mature specimens not or scarcely gelatinized.

*Type species:* *G. tomentosus* Murr.

*C. tomentosus* (Murr.) O.K. Miller; *C. leptocystis* (Sing.) O.K. Miller; *C. sibiricus* (Sing.) O.K. Miller; *C. helveticus* (Sing.) Moser in Gams with at least two subspecies; obviously also *C. loculatus* O.K. Miller.

Sect. 2. *CHROOGOMPHUS*. (*Viscogomphus* Imai 1938 ut sect. *Gomphidi*). Pileus viscid, shining when dry in most of the individual carpophores, neither tomentose nor fibrillose when mature; epicutis of mature specimens distinctly gelatinized.

*Type species:* *G. rutilus* (Schaeff. ex Fr.) Lundell & Nannfeldt.

*C. vinicolor* (Peck) O.K. Miller [with ssp. *californicus* (Sing.) Sing.]; *C. jamaicensis* (Murr.) O.K. Miller; *C. flavipes* (Peck) O.K. Miller; *C. rutilus* (Schaeff. ex Fr.) Lundell & Nannfeldt (*Gomphidi* viscidus (L. ex) Fr. non Pers.) (with ssp. *alabamensis* (Earle ex) Sing. and spp. *michoacanensis* Sing. & Kuthan); *C. superiorensis* (Kauffm. & Smith) Sing.; *C. ochraceus* (Kauffm.) O.K. Miller with ssp. *fulmineus* (Heim) Sing.\*; obviously also *Gomphidi* *purpurascens* Vasilieva (unless too close to one of the preceding species).

## GENERA INCOMPLETELY KNOWN

*Gymnogomphus* Fayod, *Prodrome, Ann. Sc. Nat., Bot.* VII. 9: 385. 1889, see p. 759.

\*c.n. (*Gomphidi* *viscidus* var. *fulmineus* Heim, *Treb. Mus. Ciènc. Nat. Barcelona*, 15: 68. 1934).

## BOLETACEAE Chevalier

*Flore Env. Paris*, p. 248. 1826 ("ordre"); R. Maire, *Bull. Soc. Bot. Fr.*, tab., 1901 (nom. nud.); *Recherches*, p. 166. 1902, both as Boletacées); Lotsy, *Vorträge*, p. 717. 1907.

Type genus: *Boletus* Dill. ex Fr. sensu Gilbert.

Syn.: *Leucosporellae* Gilbert, *Bolets*, p. 100. 1931.

*Gyrae* Gilbert, *Bolets*, p. 102. 1931.

*Gyrodontaceae* (Sing.) Heinemann, *Bull. Jard. Bot. Etat, Bruxelles* 21: 228. 1951.

*Strobilomycetaceae* Gilbert, *Les Bolets*, p. 83, 105. 1931. ("*Strobilomycetaceae*"); Sing., *Ann. Myc.* 34: 324. 1936.

*Ixechinaceae* Guzmán, *Bol. Soc. Mex. Mic.* 8: 59. 1974.

*Meiorganaceae* Heim ex Jülich, *High. Taxa Basid.*, p. 378. 1981.

*Boletellaceae* Jülich, l.c. p. 357. 1981.

*Xerocomaceae* (Sing.) Pegler & Young, *Trans. Brit. Myc. Soc.* 76: 112. 1981.

**Characters:** Pileus scaly, fibrillose, mealy, tomentose, granulose, velutinous, or glabrous, often becoming tesselate-rimose, viscid or dry, small to large, the margin sometimes projecting; hymenophore tubulose, rarely lamellate (in *Phylloporus* and *Phylloboletellus*; also in a form of *Chalciporus piperatus*); tubes short to long, decurrent or adnate to depressed around the stipe, or free; pores very small or closed when quite young to very wide and open from the beginning, sometimes lamellately arranged ("boletinoid"), and then tubes less easily separated from the context of the pileus, usually very easily separable from the context, discolored, or more frequently concolorous with the pores, whitish to sordid, or whitish to yellowish, or yellow to golden yellow, more rarely orange to red, the pores sometimes orange to red or reddish brown, at last often olivaceous or yellowish brown, sometimes becoming dirty livid or blue to green or brown on pressure; spore print pale olivaceous to deep olivaceous, cinnamon, or fawn color to vinaceous pink, or ochraceous, or lemon yellow; spores usually not very richly colored under the light microscope even when quite mature (except in *Xanthoconium* where they are bright golden), most frequently pale melleous or brownish melleous, or pale yellowish, even hyaline, smooth or ornamented with moderately thickened wall, which rarely reaches more than 1  $\mu\text{m}$  in diameter, their length rarely over 20  $\mu\text{m}$  usually well below 20  $\mu\text{m}$ , with or without germ pore or callus, globose, subglobose, short-ellipsoid to ovoid, fusoid-subcylindric, fusoid-ellipsoid, ovoid-fusoid (clavate), or cylindric, cyanophilic, uninuclear; basidia and cystidia usually comparatively small, more rarely large; hymenophoral trama more or less bilateral in youth, in some genera with less striking bilaterality (*Phylloporus*-subtype); interlaced hymenopodium usually little or not developed; hyphae with or without clamp connections; stipe usually fleshy and central, cylindric, attenuate or thickened toward the base, or ventricose to bulbous, smooth and glabrous or ornamented with glandulae, with furfuraceous floccons, with scabrous squamules, or with reticulate lines, solid to hollow; veil often present and then membranous, or membranous-floccose, or glutinous, or pulverulent (and then mostly yellow), either fugacious or persistent as an annulus. Pulvinic acid derivatives like variegatic, xerocomic, atrotomentinic acid and other groups of chemically defined pigments - some of these in the older literature often referred to as boletol - mostly present in the carpophores and/or

mycelial cultures, and their distribution characteristic for the various genera and sections. On earth, more rarely on decayed wood or sawdust, rarely parasitically on Gasteromycetes or tree roots, the majority symbiotic with forest trees forming obligatory or facultative ectomycorrhiza.

**Limits:** The delimitation of the Boletaceae from the related families of Boletineae (Paxillaceae, Gomphidiaceae) is obvious in the key (p. 718) and will also be discussed wherever a problem of delimitation arises. Some gastroid genera (especially *Gastroboletus*, see p. 16, 124 and 844) are very close or similar to the Boletaceae but differ in their inability to project the spores by autobasidia; they do not produce a spore print under any conditions. All pore-bearing Agaricales which do not belong to the Boletaceae have spore hilums of the nodulose, not the open-pore type and do not combine uninucleate spores and colored spore walls (and spore print colors occurring in the Boletaceae) with monomitic trama.

The taxonomy of the Boletineae, and especially the Boletaceae has been re-evaluated by me (*Persoonia* 11: 269-302. 1981) on the basis of new evidence. This paper should be consulted with regard to the delimitation of the Boletineae and Boletaceae as well as the taxa belonging to them. The most important change, compared with the 1st to 3rd edition of the present work is the abandonment of the family Strobilomycetaceae.

Of the genera placed in Boletaceae and Boletellaceae by Jülich (1981) (22 in total) four do not belong, two are synonyms, and one is misspelled. The three families admitted by him (Boletaceae, Boletellaceae, and Strobilomycetaceae) are separated by spore ornamentation only; Gyrodontaceae and Meiorganaceae are added because of clamped hyphae, but these occur in his Boletellaceae also. Even if the dismemberment of Boletaceae into five families were taxonomically justified, the families, as described and exemplified, are poorly described, overlapping and certainly not natural.

## KEY TO THE SUBFAMILIES



\*“bright ferruginous” according to Corner in *B. hibiscus* Corner which otherwise is similar to *P. tropicus*, but was the color observed in fresh print?

totally absent or extremely rare, or present only in the mycelium but absent in the hyphae of the carpophore; spores non-elongate only if clamp connections are absent in the carpophore.

C. Clamp connections in the carpophores present; stipe with veil, often hollow; pileus dry and squamose; obligatory ectomycorrhiza with conifers (see *Suilloideae*).

C. Clamp connections absent (possibly present in the mycelium of some species) or veil absent.

D. Hymenoporal trama of the *Boletus*-type; hymenophore strictly tubulose or boletinoid; NH<sub>4</sub>OH and NH<sub>3</sub> reacting pink, reddish lilac, gray, green, or negative on context of the pileus, not ever, even fleetingly, blue or green-blue on the surface of the pileus unless the spore print is pink or brownish pink when fresh.

E. Stipe with a distinct covering of glands consisting of fascicles or bunches of cystidia which tend to be or become incrusted by a colored resinous incrustation, or else, if these glands are absent, with a membranous but often on the outside glutinous (not throughout glutinous) veil, or combining strictly adnate to adnato-subdecurrent hymenophore with strongly viscid pileus and obligatory ectomycorrhiza with conifers (mostly *Pinus*); hymenophore never (including inside of the tubes) colored pink, carmine red, reddish-cinnamon unless the stipe is annulate; cystidia generally, at least in age and in their majority, incrusted by a resinous mass; hymenophore never lamellate throughout; spores always elongated and smooth; ectomycorrhiza with conifers.

*Suilloideae*, p. 748

E. Glands absent on the stipe (but minute flocculi or scabrosities with dermatocystidia other than those described above often present); spores smooth or ornamented; hymenophore tubular or lamellate (if lamellate either spores longitudinally winged, or hymenophore (not only pores) entirely reddish (fresh), either adnate (or even subdecurrent or ± strongly depressed around the stipe; veil, if present, either membranous (outside glutinous or not), or membranous-dry, or entirely glutinous, or arachnoid-flocculose; ectomycorrhiza with conifers or with dicotyledonous trees.

F. Spore print fresh dark brown to fuliginous-brown (almost blackish); spores ornamented, usually rather short ( $Q = 1-2$ ); yellow pigments in the hymenophore absent or diluted, in the context and stipe and on the pileus absent; pileus never red, but mostly soon gray to blackish squamose; veil generally present, not glutinous; context often reddening and eventually blackening; tyrosine - Dopa - melanines typically present.

*Strobilomycetoideae*, p. 800

F. Spore print different; not combining the other characteristics indicated above.

*Boletoideae*, p. 765

D. Hymenoporal trama of the *Phylloporus*-type (hyphae of the lateral trama not recurved and but slightly divergent, mostly not or not strongly differentiated in pigmentation from the mediostratum) or intermediate between the *Boletus*- and *Phylloporus*-type (but then either not obligatorily ectomycorrhizal or habit of *Xerocomus subtomentosus* with dry pileus and context unchanging).

G. Hymenophore tubular (and then often with lamellarily extended tube walls around the stipe) or lamellate, mostly ± adnate otherwise, with narrow (but never stuffed) pores or with wide pores; NH<sub>4</sub>OH and NH<sub>3</sub> often strongly reacting blue on fresh pileus surface; veil none; hymenophore not arcuate-decurrent and not red; setoid cystidia present or absent.

*Xerocomoideae*, p. 757

G. Hymenophore always tubular (except in one exceptional case), reddish (cinnamon) throughout and the basal mycelium yellow or hymenophore arcuate-decurrent and/or surfaces pulverulent, rugose, or viscid (see "F" above).

### Subfamily Gyroporoideae Sing. ex Sing.\*

*Persoonia* 11: 296. 1981 nom. nud.; Sing. (see below).

Type genus: *Gyroporus* Quél.

\*Sporis ellipsoideis, levibus sed microscopii elecronici ope asperulis, in cumulo flavidis. Typus: *Gyroporus* Quél.

Spores ellipsoid, rarely over 2 times longer than broad, smooth under the light microscope, EM-asperulate, in mass "colonial buff", "amber yellow", "citron yellow"; hymenophoral trama of the *Boletus*-type; stipe of adult carpophores frequently hollow; hyphae of the carpophore and mycelium with clamp connections (rarely in apparently parthenogenetic specimens without clamp connections); context if bluing producing gyrocyanin (as *Chamonixia*); ectomycorrhiza with a wide range of trees.

### 203. GYROPORUS Quél.

*Enchiridion* p. 161. 1886.

Type species: *G. cyanescens* (Bull. ex Fr.) Quél.

Syn.: *Suillus* Karst., *Bidr. Finl. Nat. Folk.* 37: v. 1882 non S.F. Gray (1821).

*Coelopus* Bat., *Bolets*, p. 12. 1908.

*Leucobolites* G. Beck, *Zeitschr. Pilzk.* 2: 146. 1923.

*Leucoconius* (Reichenb.) G. Beck, l.c.

**Characters:** Those of the subfamily; pileus non-viscid, glabrous to coarsely fibrous-subsquamose; cuticle made up of repent to ascendant elongate but sometimes rather short and thick hyphae with thin or thick walls; terminal members often cystidioid and in palisade (Pl. 76,1); hymenophore tubulose with concolorous small to more often medium sized to large pores, depressed around the stipe, rather long, white, pink, or pallid-stramineous; spore print yellow ("Colonial buff", "amber yellow", "citron yellow" Ridgway); spores (Pl. 76,4) stramineous-subhyaline to yellowish, ellipsoid, rarely more elongate than twice as long as broad, of medium size but rather variable in this regard; cystidia present in the tubes and on the pores (Pl. 76,2); hymenophoral trama bilateral, of the *Boletus* type; stipe hollow or solid, its surface glabrous or fibrous, or subfurfuraceous, not reticulate, without glandular dots, without veil, without pseudosclerotium; context white or whitish, unchanging or bluing (gyrocyanin) by autoxidation; hyphae of the carpophore (except in rare parthenogenetic aberrations) constantly with clamp connections; the usual inorganic reagents causing little or no color reactions. On the ground under conifers and frondose trees normally forming ectomycorrhiza, but possibly sometimes fruiting without mycorrhizal association.

**Development of the carpophores:** Probably metavelangiocarpous and pileostipitocarpous (Reijnders) in the two European species, thus apparently like the Gomphidiaceae which, however, are stipitocarpous like *Strobilomyces*.

**Area:** Both in temperate and tropical regions, widely scattered but uncommon or absent in the southern temperate zone.

**Limits:** The combination of yellow spore print color and short spores makes it possible to distinguish even the rare parthenogenetic forms from all other boletes with a hymenophoral trama of the *Boletus*-type and dry pileus and stipe. According to Corner (1972) the stipe trama consists (in contrast to other boleteaceous genera) of

transverse hyphae. This indication, much exaggerated, was originally an elaboration of Reijnders's finding that the stuffed interior of the stipe of *G. cyanescens* shows a surprising number of hyphae running horizontally. The rind itself is described as interwoven ('hyphes ... emmêlées') in an early stage and remaining so for a long time. Reijnders (1968) explains this structure as a consequence of the hollowing by expansion observed in the stipe, accompanied by an outer veil layer strictly appressed to the cortex of the stipe and of similar structure. It is Corner (1972) who adds that he recognized *Gyroporus* as a genus not (in contrast to Arpin & Kühner) because of its spore color or the presence of clamp connections but because the stipe is not longitudinally fissile and not constructed by longitudinal hyphae but splitting transversely and being constructed by hyphae that have grown transversely round and across the longitudinal axis. This statement is apparently not based on Reijnders's careful observations but on observations on the Malaysian species *G. malesicus* (where the transversal fissibility of the stipe may have something to do with the series of vertically superimposed cavities in the specimen illustrated which is the smallest known in *Gyroporus*). The stipe sections (a and b, p. 55) do not prove transversal arrangement of the surface hyphae of the stipe. As for other species of *Gyroporus* Corner merely states that 'several species ascribed to *Gyroporus* may not belong because their stems appear to be longitudinally scissile, e. gr. *G. atroviolaceus*', a species I have studied and find to belong to *Gyroporus* (Singer 1977). Arpin & Kühner (1977) merely translate Corner's statement and imply that it is valid also for *G. cyanescens* and *G. castaneus*, not commenting on the extra-European species *G. malesicus* and *G. atroviolaceus*.

Do then the anatomical features of the type of *Gyroporus* really agree with Corner's characterization? According to my own observations, I agree with Arpin & Kühner that the consistency of the stipe rind is undoubtedly due to a special structure, but this structure is not the one described by Corner. In *G. castaneus*, for example, longitudinal and transverse sections of the stipe show that the interior layer of the stipe trama is influenced by the horizontal pull exercised by the widening of the stipe which leads to horizontal stretching of some hyphal strands. This stretching causes air spaces to appear between hyphal strands and single hyphae, and finally these dissociate to such a degree that the cavity results whereby many of the remaining hyphae collapse. Further towards the stipe surface we find a rather thin layer of tissue which is composed of two elements (1) longitudinally arranged hyphae and strands of hyphae running vertically and parallel with each other or almost so, intermingled with (2) strongly interwoven, irregularly arranged hyphae. This structure is a result of the intermingling of the interwoven hyphae (growing at first almost horizontally outwards as in most boleti) of the external velar layer with the longitudinal-vertical hyphae of the subjacent rind layer. For reasons of a somewhat different development as compared with other hollow-stemmed boletes (*Boletinus*, *Pulveroboletus*), this structure of *G. castaneus* is not exactly the same as in the other genera where in the stipe context longitudinal hyphae predominate. A supplementary analysis of the stipe anatomy in *G. cyanescens* and *G. purpurinus*, showed me an analogous picture, only that in *G. cyanescens* with a more extensive original velar

layer, the prevalence of interwoven hyphae is stronger. These data complement those given by Reijnders and contradict those provided by Corner. Whether the stipe is longitudinally fissile or not seems to depend on the prevalent stretching direction of the stipe tissue, the thickness of the rind layer compared with the velar layer, and possibly the extension of the cavity or cavities at a certain stage of development. The position of the genus *Gyroporus* side by side with *Strobilomyces* is highly unsatisfactory, even if the type of development in both genera is supposed to be the same.

The EM structure of the outer spore wall ("exosporium" of Perreau) is almost identical in *Gyroporus cyanescens*, *G. castaneus* and *Phlebopus colossus* (J. Perreau, *Bull. Soc. Myc. Fr.* 97: 135-142. 1981).

If we, nevertheless, separate the Gyroporoideae from the Gyrodontoideae since 1981, we do this with particular reference to pigment-chemistry [presence of gyroporin, gyrocyanin (Bresinsky et al. 1974) in Gyroporoideae whereas *Gyrodon lividus*, type of the Gyrodontoideae, lacks gyroporin-gyrocyanin, and contains, instead, variegatic acid and variegatorubin (Bresinsky & Orensi 1970)].

*State of knowledge:* Out of ten species belonging to *Gyroporus*, seven are completely known to this author.

*Practical importance:* All species are edible and highly estimated by mycophagists.

## SPECIES

*G. subalbellus* Murr. (*Suillus*, Sacc. & Trotter; *G. roseialbus* Murr.); *G. umbriniscamosus* Murr.; *G. cyanescens* (Bull. ex Fr.) Quél. (*Boletus*, Fr.; *Suillus*, Poiret in Lam. ex Karst.); *G. phaeocyanescens* Sing. & Ivory in Sing., Araujo & Ivory; *G. purpurinus* (Snell) Sing.; *G. castaneus* (Bull. ex Fr.) Quél. (*Boletus*, Fr.; *Suillus*, Poiret in Lam. ex Karst.); *G. atroviolaceus* (Hoehnel) Gilbert (*Suillus*, Hoehn.); perhaps also *G. earlei* Murr.; apparently also *G. punctatus* L. Vasilieva and *G. heterosporus* Heinemann (unless too close to *G. castaneus*).

## Subfamily Gyrodontoideae Sing.

*Farlowia* 2: 230. 1945.

*Type genus: Gyrodon* Opat.

*Characters:* Hyphae with clamp connections; spores ellipsoid or globose, olive-brownish; hymenophore rarely typically boletinoid; spores short.

## KEY TO THE GENERA

- A. Veil present.
- A. Veil absent.

204. *Paragyrodon*, p. 743

- B. Hymenophore soon depressed around the stipe which is large and central. 205. *Phlebopus*, p. 743  
 B. Hymenophore more or less arcuate-decurrent and/or stipe eccentric or strongly reduced to absent.  
   C. Spores larger than 5  $\mu\text{m}$ ; spore print brown with an olive hue; stipe usually well developed, central to lateral. 206. *Gyrodon*, p. 745  
   C. Spores smaller than 5  $\mu\text{m}$ ; spore print with a purplish hue; stipe non. 207. *Meiorganum*, p. 746

## 204. PARAGYRODON (Sing.) Sing.

*Ann. Mycol.* 40: 25. 1942.

*Type species:* *P. sphaerosporus* (Peck) Sing.

*Syn.:* *Gyrodon* subg. *Paragyrodon* Sing., *Rev. Mycol.* 5: 7. 1940.

*Characters:* Hymenophore decurrent; spore print olive brown (so seen on typical material under oak in Lincoln, Nebr. 1953, on white paper; Watling indicated the spore print as "anilin yellow", perhaps in thin layer); spores subglobose; cystidia conspicuous; stipe with a volva-like annulus which is viscid, white and membranous; hyphae with clamp connections, inamyloid. On the ground near trees with which it appears to form ectomycorrhiza.

*Development of the carpophores:* Unknown; either "hemiangiocarpous" or "pseudoangiocarpous", more probably the former.

*Area:* North America (from Michigan to Minnesota and Nebraska).

*Limits:* This species and genus is easily recognized and sufficiently well delimited from other Gyrodontoideae. Smith & Thiers (1964, 1971) transferred it to *Suillus*, not a surprising attitude since they consider *Gyrodon lividus* likewise as close to or identical with (their version of) *Suillus*. Watling (1969) wishes to maintain the genus *Paragyrodon* but transfers it to the Suilloideae because of the "configuration of the hymenophoral tissue" (whatever this is meant to express). All Suilloideae with clamp connections differ from *Paragyrodon* in the elongated spores, a different type of veil, or else no veil at all, more boletinoid hymenophore, and association with trees other than Fagales.

*State of knowledge:* Only one species is known at present.

*Practical importance:* Unknown.

## SPECIES

*P. sphaerosporus* (Peck) Sing.

## 205. PHLEBOPUS (Heim) Sing.

*Ann. Myc.* 34: 326. 1936.

*Type species:* *Boletus (Phlebopus) colossus* Heim.

*Syn.: Boletus* subgen. *Phlebopus* Heim, *Rev. Myc.* 1: 9. 1936.  
*Phaeogyroporus* Sing., *Mycologia* 36: 360. 1944.

**Characters:** Differs from *Gyroporus* macroscopically by its olive brown to brown-olive spore print ("Isabella color", "light brownish olive" (Ridgway), its spores under the microscope being smooth, and brownish (light microscope), the stipe never hollow; not forming ectomycorrhiza or forming facultative ectomycorrhiza or some other type of mycorrhiza, sometimes forming cryptas.

**Development of the carpophores:** Unknown, probably gymnocarpous.

**Area:** Pantropical and subtropical.

**Limits:** The genus is obviously more closely related to *Gyrodon* than to *Gyroporus*. It differs from *Gyrodon* by its hymenophore which is less "gyroid" (pores more subisodiametric, narrow, more rarely wide) and is either from the beginning or becomes at full maturity distinctly depressed around the stipe. Perreau's EM studies of the spores (1981) suggest that the spores of *Phlebopus* have typically the same ultra-structure as those of *Gyroporus*, but at least the type species of *Gyrodon* has EM-smooth spores. Some species of *Gyrodon* are obligatorily ectomycorrhizal while this has never been claimed for any species of *Phlebopus*. The non-mycorrhizal species of *Gyrodon* tend to have eccentric stipes.

**State of knowledge:** The type species was until recently incompletely known and the genus was therefore redescribed with another type species under the name *Phaeogyroporus* Sing., widely used until an authentic specimen of *P. colossus* Heim (P) was discovered by J. Perreau (1981) and sent to Heinemann who has designated it "lectotype". Since it agrees in everything including spore measurements with Heim's original description and illustration (see Heinemann & Rameeloo 1980) the name *Phlebopus* can now be considered to be rehabilitated.

A key to the nine well known species belonging to *Phlebopus* has been published by Singer, Araujo & Ivory, *Nova Hedwigia* Beih. 77: 40-47. 1983.

**Practical importance:** *P. tropicus* has been shown to form a mycelium crust around the roots of species of *Citrus* in Brazil covering colonies of *Pseudococcus comstocki* which attack the roots of these plants after they have been carried there by the ants (*Solenopsis saevissima* var. *moelleri*); these mycelial crusts are called criptas by the Brazilian writers, and the author has adopted the term cryptas for English usage. The *Pseudococcus* living in symbiosis with the fungus is thought to be the immediate reason for the subsequent dying of the trees affected, but the action of an endotrophic mycorrhizal fungus weakens the plant sufficiently, before the attack of the *Pseudococcus* takes place. This extremely complicated and interesting cooperation of fungi and animals in symbiosis, epibiosis and parasitism has been described, illustrated, and discussed by Gonçalves and Milanez (*Rodriguesia* 4: 179-263. 1940). The combination of basidiomycetous cryptas and *Pseudococcus* is, by the way, strikingly analogous in the disease called phytrosis of coffee, where the fungous pathogen is now known to be *Diacanthodes philippinensis*.

*P. braunii* is edible.

## SPECIES

*P. tropicus* (Rick apud Rehm & Rick) Heinemann & Rammeloo; *P. braunii* (Bres.) Heinemann (Boletus, Bres\*; Phaeogyroporus, Sing.; Boletus bruchii Speg.; Phlebopus, Heinemann & Rammeloo; Phlebopus harleyi Heinemann & Rammeloo); *P. silvaticus* Heinemann; *P. portentosus* (Berk. & Br.) Boedijn; *P. sudanicus* (Har. & Pat.) Heinemann; *P. colossus* (Heim) Sing.; *P. beniensis* (Sing. & Digilio) Heinemann & Rammeloo (vix sensu Hein. & Ram.); *P. brasiliensis* Sing. in Sing., Araujo & Ivory; apparently also *P. latiporus* Heinemann & Rammeloo (but probably identical with *P. tropicus*) and *P. brunneoruber* (Beeli) Heinemann & Rammeloo (if clamp connections present\*\*).

### 206. GYRODON Opat.

*Comm. Hist.-nat. fam. Fung. Bolet.*, Wiegmann's Archiv 2: 5. 1836.

Type species: *G. sistotremoides* (Fr.) Opat. \*\*\*

Syn.: *Uloporus* Quél., Enchiridion p. 162. 1886.

*Campbellia* Cooke & Mass., Grevillea 18: 87. 1890, non Wight (1850).

*Rodwaya* Sydow, Hedwigia 40: (2). 1901, non Muell. (1890).

*Boletinellus* Murr., Mycologia 1: 9. 1909.

*Plicaturella* Murr., N. Am. Fl. 9: 172. 1910 sec. Ginns & Redhead.

*Gilbertina* Heim, Rev. Mycol. 31: 151. 1966.

*Pseudogyrodon* Heinemann & Rammeloo, Bull. Jard. Bot. Nat. Belg. 53: 295. 1983.

**Characters:** Pileus not quite glabrous, inclining to become viscid in wet weather; hymenophore consisting of irregularly arranged (gyrose) or boletinoid tubes or honey-combs, arcuate-decurrent; spore print brown to olive ("willow" M. & P.); stipe not reticulate, not hollow, not glandulose, central or eccentric (Pl. 1,2) without a veil, without a pseudosclerotium, not forming cryptas; context either changing color or unchanging on exposure; spores short-ellipsoid to subreniform-phaseoliform (but very short), smooth, brownish; cystidia present or only as cheilocystidia on the pores, and even these very inconspicuous; hyphae with clamp connections. On wood or on the ground in woods, often forming mycorrhiza with trees such as *Alnus*, *Fraxinus*, *Allophylus*, rarely *Quercus*.

\*The holotype is lost, but diagnosis and illustration make it clear enough that this is a young *Phlebopus* (hence smaller spores and ± decurrent hymenophore), conspecific with the only West African species known.

\*\*Heinemann & Rammeloo now describe this species as clamp-less (1982); but since Heinemann (1954) also described a specimen cited by him (K) for *P. sudanicus* as clampless which was found to have clamped hyphae by me, the position of *P. brunneoruber* remains doubtful.

\*\*\*Singer (1951) has studied authentic material of *B. sistotremoides* Fr. which proves that this is the same as *G. lividus*. Whatever Fries suspected about the position of this fungus cannot change the evidence obtained through an analysis of the scarce and valuable classical herbarium material left to us, inasmuch as such speculations about Fries's vacillations led to regrettable upsets in the nomenclature of the species involved and do not conform with the type concept in present nomenclature. For this reason, the replacement of *Gyrodon* by *Uloporus* must be rejected, inasmuch as *Uloporus* Quél. is a superfluous name (Art. 63.1).

*Development of the carpophores: Gymnocarpous in G. lividus.*

*Area:* Almost cosmopolitan.

*Limits:* These are obvious from the key, p. 742, and need no further explanation. But care should be taken not to confuse other genera with the general appearance of *Gyrodon* but without clamp connections. These are likely to belong to *Pulveroboletus*, sect. *Sulphurei*. Young carpophores of certain species of *Phlebopus* might be looked for in *Gyrodon*.

In contrast to Heim, Smith & Thiers (1971) consider *Gyrodon meruloides* as generically different from *Gyrodon lividus* (which A.H. Smith thinks is a *Suillus*) and separate the former under the generic name *Boletinellus*. Since they fail to key the genus out (p. 26-27) and to explain why *Boletinellus* is "not at all closely related to *Gyrodon*" (p. 294), I cannot comment.

As for *Rodwaya* and *Gilbertina* see under *Meiorganum*.

*State of knowledge:* Ten species are well known. Some more are possibly congeneric but incompletely known.

*Practical importance:* Some species are edible but they are not popular as food. Some have a potential significance as mycorrhizal fungi in forestry.

## SPECIES

*G. intermedius* (Pat.) Sing. (*Phylloporus*, Pat.; *Boletus*, Sacc.; *Boletinellus*, Gilbert); *G. proximus* Sing.; *G. rompelii* (Pat. & Rick) Sing. (*Phylloporus*, Pat. & Rick); *G. meruloides* (Schw.) Sing. (*Daedalea*, Schw.; *Boletinellus*, Murr.; *Paxillus porosus* Berk. in Lea; *Boletinus*, Peck); *G. lividus* (Bull. ex Fr.) Sacc. [*Boletus*, Fr.; *Uloporus*, Quél.; *Gyrodon sistotremoides* (Fr.) Opat.; *Boletus rubescens* Trog.; *Boletus sistotrema* Fr. sensu Rostkovius]; *G. monticola* Sing.; *G. exiguum* Sing. & Digilio; *G. africanus* (Cooke & Mass.) Sing.; *G. cupreus* Heinemann; *G. adisianus* Sing. ined.; obviously also *Rodwaya infundibuliformis* (Cooke & Mass.) Sydow.

## 207. MEIORGANUM Heim

C. R. Acad. Sc. Paris 261: 1720. 1965; Rev. Mycol. 31: 157. 1966.

*Type species:* *M. neocaledonicum* Heim.

*Characters:* Pileus glabrous, not viscid; hymenophore consisting of at first gyrose anastomosing lamellae which become more tubular-boletinoid with pores mostly or almost isodiametric; dented-sinuate, shallow (1-1.4 mm deep), not separable from the context; spore print gray-brown-lilac-purple according to Heim; stipe none; pileus at first turbinate then laterally attached (or somewhat dorsally extended); context soft, fleshy-spongy, bluing on exposure; spores short ellipsoid to ellipsoid, often reniform when seen laterally, smooth, light brown, small (to 5 µm long), with

homogeneous 0.2-0.35  $\mu\text{m}$  thick wall which is inamyloid, cyanophilic; cystidia present as pleuro- and cheilocystidia, often with internal bodies; hymenophoral trama bilateral; hyphae with clamp connections, in dried material often showing blue (in NH<sub>4</sub>OH) granulations; these bluish fuliginous in Melzer's reagent but bright blue when the iodine is reduced by ammonia; in ammoniacal medium, a porphyry gray pigment enters the medium whereby floating spores become discolored (if the spores are studied in Melzer's reagent after hydrolysis in ammonia, they may erroneously be interpreted as amyloid). On wood (*Agathis*).

*Development of the carpophores:* Gymnocalypous (Corner 1971).

*Area:* New Caledonia, Malaya.

*Limits:* Heim has studied a fragment of the type of *Campbellia infundibuliformis*, but neither his data nor those published by the original authors justify an approximation of this species to *Meiorganum* whose type (or rather a para- and topo-type probably rising from the same mycelium as the holotype) I have been able to study thanks to the amability of Dr. Heim. Everything would indicate that *Campbellia infundibuliformis* is congeneric with *Gyrodon* - as is *C. africana* - and that the eccentricity or even laterality of the stipe is not a sufficient character to separate genera in the Gyrodontoideae inasmuch as Heim himself does not question the congenericity of the - often eccentric - *G. meruloides* with *G. lividus*. Even before Heim had studied *C. africana*, I had published a South American species of *Gyrodon*, *C. exiguis*, which has likewise lateral and often strongly reduced stipe. If *C. africana* really were a genus apart, it would have to be renamed - *Rodwaya* and *Campbellia* are homonyms - (provided *C. africana* is the lectotype of *Rodwaya*, cf. *Taxon* 5: 30-33, 1956); if, as other authors insist, *C. infundibuliformis* were the type of *Campbellia* and not congeneric with *Gyrodon*, the genus *Gilbertina* would stand. Yet the question is moot since both species are congeneric with *Gyrodon*. *Meiorganum* however, although in my opinion not justifying the erection of a new family (Meiorganacés Heim) is obviously different from *Gyrodon* and easily delimited from it because of the size and color of the spores. Nevertheless, I can see no convincing evidence for any relationship of this genus with the polypores (in whatever sense of the word) since the presence of clamp connections and pleurotoid habit are often simultaneously observed in several families of the Agaricales, including the Gyrodontoideae (Pl. 1,2). I have observed medallion clamps in *Meiorganum* but these occur in many groups of the Agaricales and Gastromycetes as well as the polypores.

I can see no close relation to the Meruliaceae (sensu Donk) nor with the Coniophoraceae (sensu Donk). Whether there is a phylogenetical link with the latter is still an open question. Corner's (1971, 1972) transfer of *Meiorganum* to the Meruliaceae is certainly not justified but a distant phylogenetic relationship between Boletineae and Coniophoraceae cannot be excluded out of hand since variegatorubin, atrotomentinic acid, xerocomic acid and variegatic acid occur in *Coniophora cerebella* and *Serpula lacrymans*.\* "It is difficult to voice an opinion on the systematic significance of this discovery" (Kühner 1977). Certainly *Meiorganum* which shares most

\*See Besl & Bresinsky, *Zeitschr. Pilzk.* 43: 311-322. 1977 (see also p. 141 of the present work).

significant characteristics with the Gyrodontoideae is neither coniophoraceous nor intermediate between Boletaceae and Coniophoraceae; the fleshy-spongy context which turns blue, the structure of the hymenophoral trama and the spore print color are those of the Boletaceae. The absence of a true stipe is the only difference (as also recognized by Corner 1971, p. 358).

**State of knowledge:** Only one species is known well enough to be compared with other genera; although the basic characters are generally known, it must be said that the structure of the hymenophore and the development of the carpophores as well as the distribution and nature of the pigments remain incompletely described. The hymenophoral trama is phylloporoid according to Corner, ± regular according to Horak, but in my material it appeared to be mainly regular with an outer narrow layer showing rameose hyphae running somewhat perpendicular to the tube wall. They are more loosely arranged and accompany the hymenium around the upper tube ends whereas the hymenophoral trama which corresponds to the mediostratum of other Boletaceae does not follow up but merely penetrates the pileus-trama above each tube-wall for a short distance. Since the mediostratum is not and the adjoining layer only slightly gelatinized, it becomes clear why the hymenophore is not easily separable from the trama as in many other Boletaceae. Whether the tramal structure as observed by us is, as one is inclined to assume, the aspect of the structure in an old or at least fully mature specimen or rather a somewhat abnormal condition, and what the precise structure of the young hymenophoral trama is must be evaluated as soon as young and well-prepared material becomes available. The species is very well illustrated by Heim (*Rev. Mycol.* 30, pl. 4-9, 1966).

**Practical importance:** Unknown.

## SPECIES

*M. neocaledonicum* Heim.

### Subfamily **Suilloideæ** Sing.

*Farlowia* 2: 250. 1945.

**Type genus:** *Suillus* Micheli ex S.F. Gray.

**Characters:** Pileus glutinous or viscid, or rarely subviscid when wet, or else non-viscid but then with boletinoid hymenophore (in the species with viscid pileus, the hymenophore is either boletinoid or non-boletinoid); stipe with glandulae, or non-glandulose with a glutinous or a fibrillose-membranous veil, or without veil (veil never pulverulent and bright yellow or green at the same time, nor completely glutinous and slimy unless the stipe is glandulose); stipe usually more or less equal, rarely ventricose or otherwise unequal, without a distinct pseudosclerotium, solid or hollow; hymenophore never completely (inside and pores) dull reddish cinnamon, deep dusky red, or pink unless veil present; hyphae with or without clamp connec-

tions. Surface of the pileus never bluing with ammonia (but context mostly strongly pink or lilac, gray or green with alkali); spores smooth; cystidia mostly resinous-incrusted; ectomycorrhiza obligatory, always with Pinaceae rarely also with Salicaceae.

**Note:** The genera of this subfamily are obviously closely related with each other, more closely than with other genera of the Boletaceae; no other genus with smooth spores except those of the Gyrodontoideae and two of the Suilloideae (*Boletinus*, *Psiloboletinus*) has clamp connections; but *Suillus* has no clamp connections in the trama of the carpophore and should therefore be compared with the genera of Boletoideae (see paragraph on limits of those genera).

#### KEY TO THE GENERA

- A. Clamp connections present in the hyphae of the trama of the carpophore; dermatocystidia forming glandular dots on the stipe absent; stipe often hollow; xerocomic acid present along with variegatic acid and variegatorubin and atromentinic acid (at least in *Boletinus cavipes*).  
B. Veil present. 209. *Boletinus*, p. 751  
B. Veil absent. 208. *Psiloboletinus*, p. 749
- A. Clamp connections absent in the hyphae of the trama of the carpophore; dermatocystidia forming glandular dots on the surface of the stipe either present or absent; stipe not hollow; pigments not as above - either different, or with different distribution.  
C. If no veil is present, the stipe is often covered by glandular dots; if no glandular dots are present on the stipe, the mycelium is always ectomycorrhizal with Pinaceae; the spores are always elongated, fusoid to cylindrical; hymenophore boletinoid or tubular and neither lamellate nor inside and out with an ochre-red, dull red, wine red, or pink color; atrottenhamic and xerocomic acid absent; pulvinic acids which in  $H_2SO_4$  become discolored - absent or present; taste mild to acid 210. *Suillus*, p. 752  
C. Veil absent; glandular dots absent; spores fusoid, cylindrical or short ellipsoid, mycorrhiza not constantly with conifers; hymenophore tubular, rarely lamellate, and containing both in the interior of the tubes and on the pores a reddish pigment; atrottenhamic and xerocomic acid present; pulvinic acids which discolor in  $H_2SO_4$  (type E of Bresinsky et al.) absent; if the taste of context is not mild it is peppery or bitter; basal mycelium always of a bright yellow color (see Boletoideae, p. 765).

#### 208. PSILOBOLETINUS Sing.

*Farlowia* 2: 250. 1945.

*Type species: P. lariceti* (Sing.) Sing.

**Characters:** Pileus tomentose, dry, with at first involute margin; spores elongated, longer than twice their breadth, smooth, rather light (brownish ochraceous) colored, with rather thin wall, generally without suprahilar appplanation or depression, in print when dehydrated between "French beige" and "burnt almond" (M & P); cystidia mostly incrusted (oleocystidium-type), rather voluminous; clamp connections present on most septa (including the basal septum of the basidia); hymenophore boletinoid with a marginal narrow lamellate zone; hymenophoral trama bilateral of the *Boletus*-type (with a melleous-hyaline to subhyaline medio-

stratum and a hyaline to subhyaline lateral stratum consisting of strongly divergent hyphae which do not touch each other); pores rather wide and somewhat compound, seriate, not discolorous; stipe hollow, no veil (nor is there an appendiculate veil on the margin of the pileus), without glandular dots; trama bluing when bruised, consisting of radially arranged hyphae in the pileus, but in the upper portion of the pileus in form of a cuticular trichodermium which becomes cutis-like in age, some hyphae hyaline, some with a colored pigment-incrustation, some transformed into oleiferous hyphae; no red pigments present when fresh; ectomycorrhiza with *Larix*.

*Development of the carpophores:* Unknown.

*Area:* Temperate zone from the Altai region to the Pacific including Sakhalin Island.

*Limits:* The genus differs from *Boletinus* in the pileus surface which consists of a 0.5 mm thick tomentose layer not broken into scales, a lamellate narrow zone along the extreme margin, the complete absence of a veil also in young specimens. It differs from *Suillus* in the presence of clamp connections (although among the numerous clamped septa some secondary septa may be occasionally observed) in the carpophore, the absence of an ixotrichodermium, the hollow stipe, and the absence of a veil in combination with association with *Larix*. It was originally considered to be a *Phylloporus* but the configuration of the hymenophoral trama, the presence of numerous clamp connections, the hollow stipe and the mainly boletinoid hymenophore connect it with the Suilloideae rather than the Xerocomoideae. It differs from all genera of the Gyrodontoideae because of the elongated spores and the mycorrhizal association with conifers. These differences have been rechecked on material kindly sent by L.N. Vassilieva, the co-collector of the type.

*State of knowledge:* Only one species is known.

*Practical importance:* As one of the ectomycorrhizal symbionts of Siberian larch, this genus has potential importance for the forester.

## SPECIES

*P. lariceti* (Sing.) Sing.

### 209. BOLETINUS Kalchbr.

*Bot. Zeitschr.* 25: 182. 1867.

*Type species:* *B. cavipes* (Opat.) Kalchbr.

*Syn.:* *Euryporus* Quél., *Enchiridion* p. 163. 1886.

*Characters:* Pileus fibrillose-squamulose or even squarrose, the fibrils and scales not superimposed upon a viscid (gelatinized) layer and therefore not easily detersile as

fragments of a veil, the surface decidedly dry even in wet weather; spores elongate, pale melleous (with occasional darker spores interspersed in a print in some specimens); cystidia rather large and mostly covered by a colored incrustation (oleocystidium-type); clamp connections constantly present in the trama of the carpophore and with clamped basidial basal septum (a few secondary septa sometimes observed); hymenophore distinctly, even very strongly boletinoid, i.e. pores rather wide at least in radial direction and more or less seriate, but without a distinct marginal lamellar zone, rather wide and more or less compound, sometimes lamellarily stretched at the stipe; stipe hollow, more rarely solid, usually cylindric or subcylindric, more rarely somewhat ventricose, constantly without glandular dots; veil constantly present but not glutinous, forming an annulus which is generally double; pigments of the pulvinic acids group present, represented by variegatic acid, xerocomic acid, variegatorubin, atrotomentinic acid, and a pigment turning blue or violet with  $H_2SO_4$ ; obligatorily ectomycorrhizal with conifers (*Larix*); context rarely turning blue by autoxidation.

*Development of the carpophores:* "Pseudoangiocarpous" in *B. cavipes* according to Kühner and in *B. paluster* according to Gentile and Snell - pilangiocarpous or mixangiocarpous and stipitocarpic according to Reijnders (1963) which is a more precise expression in Reijnders' terms.

*Area:* Circumpolar in the north-temperate zone within the area of the genus *Larix* and in larch plantations.

*Limits:* *Boletinus* differs from *Suillus* in the presence of clamp connections. The stipe is hollow, more rarely (in one species where the pileus is red and the pores particularly wide) solid, always veiled and without glandular dots, the pileus without a viscid glutinous layer, even in age, and the pigment distribution is quite different from that in all known species of *Suillus* (Bresinsky & Orendi 1970; Bresinsky & Rennschmid 1971). The chemical nature and distribution of pulvinic acid derivatives is taxonomically very important in boletes and bolete-like families, particularly in the delimitation of *Suillus* and its sections. This chemotaxonomic approach has consistently confirmed the bolete taxonomy elaborated by me, particularly as far as *Boletinus*, *Suillus*, *Phylloporus*, *Paxillus*, and *Hygrophoropsis* is concerned.

*State of knowledge:* Three species are now completely known.

*Practical importance:* As obligatory ectomycorrhiza-formers, the Boletini are of importance to the forester especially as far as larch is concerned.

## SPECIES

Sect. 1. *BOLETINUS* (*Cavipedes* Sing. 1938). Stipe hollow in mature specimens; pores wide.

*Type species:* *B. cavipes* (Opat.) Kalchbr.

Subsection *Boletinus* (*Alutaceini* Sing. 1948). No red pigment present. Fresh spore print with olive hue.

*Type species: B. cavipes* (Opat.) Kalchbr.

*C. cavipes* (Opat.) Kalchbr. with varieties and forms.

Subsection *Rubrini* Sing. (1938). Pileus red; spore print "burnt umber" to almost "chutney", or between "Cochin" and "kis kilim" (M & P).

*Type and only known species: B. asiaticus* Sing.

Sect. 2. *PALUSTRES* Sing. (1938). Stipe not hollow in mature specimens; pores extraordinarily wide especially in proportion to the relatively small carpophores. Spore print purplish brown, without an olive tinge when fresh. North American.

*Type (only known) species: B. paluster* (Peck) Peck.

## 210. **SUILLUS** Micheli ex S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 646. 1821; em. Snell (1942).

*Type species: S. luteus* (L. ex Fr.) S.F. Gray.

*Syn.: Pinuzza* Micheli ex S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 646. 1821.

*Rostkovites* Karst., *Rev. Myc.* 3: 16. 1881.

*Cricunopus* Karst., l.c.

*Boletus* Dill. ex Fr. sensu Karst., l.c., p. 17, non S.F. Gray (1821).

*Viscipellis* Quél., *Enchir.*, p. 155. 1886.

*Versipellis* Quél., l.c., p. 157, p.p.\*

*Gymnoporus* (Quél.) Quél. apud Moug. & Ferry in Louis, *Flore Vosg.* p. 476. 1887.

non *Gymnoporus* (Pers. ex) S.F. Gray (1821).

*Ixocomus* Quél., *F. Mycol.*, p. 411. 1888.

*Boletopsis* Henn. in Engler & Prantl, *Nat. Pfl. fam.* 1 (1\*\*): 194. 1898, non Fayod (1889).

*Solenia* Hill ex O. Kuntze, *Rev. Gen Plant* 3(2): 521. 1898. non (Agardh) Agardh (1924) nec Hoffm. ex Fr. (1821) nec Pers. ex Fr. (1822).

*Fuscoboletinus* Pomerleau & A.H. Smith, *Brittonia* 14: 156. 1963

*Characters:* Pileus glabrous or fibrillose-squamulose or squamulose, the fibrils or scales superimposed above a gelatinized layer, more rarely innate, detersile or not, the surface dry or viscid to glutinous; spores elongate, pale melleous to brown; cystidia rather large and mostly covered by a colored incrustation (oleocystidium-type); clamp connections none or extremely scarce in the carpophore, sometimes present in the mycelium; hymenophore never entirely dull reddish, wine red, or pink but white, gray, yellow or orange, not lamellate, but often boletinoid, pores small or wide; stipe solid, usually cylindric or subcylindric, more rarely somewhat ventricose, with or without glandular dots; veil present or absent, dry or glutinous, often forming an annulus or merely a velar appendiculation on the margin of the pileus; pigments of the pulvinic acids group present, represented by either variegatic acid and variegatorubin or by a pigment turning blue or violet in  $H_2SO_4$ ; grevellins often present; gomphidic acid absent; xerocomic acid in carpophores generally absent but

\*The type of *Versipellis* is *V. variegata* (Sw. ex Fr.) Quél. (see *Farlowia* 2: 82. 1945). If "*Boletus sub-tomentosus* E.M. Fries" is accepted as type of *Versipellis*, as assumed in the Code (*Regn. veg.* 111: 300. 1983), *Versipellis* would become a synonym of *Xerocomus* (nom. conserv.).

mostly present in mycelium cultures; obligatorily ectomycorrhizal with Pinaceae, rarely also with Salicaceae, not with Fagales; context sometimes turning blue by autoxidation. Pl. 76,5-10.

*Development of the carpophore:* Either gymnocarpous (e. gr. in *S. bovinus*) or pilangiocarpous or mixangiocarpous and stipitocarpic.

*Area:* All over the area of Pinaceae in the northern hemisphere, some species entering the tropical (but usually montane) zone in the palaeo- as well as neotropics, but predominantly temperate; a few species adventitious with pine in pine plantations outside the natural area of Pinaceae.

*Limits:* *Suillus* is here understood as delimited by Singer (1967, p. 139-140) whereby some groups which were earlier considered to be congeneric with *Boletinus* have been transferred to *Suillus*, viz. all those species without clamp connections. Smith & Thiers (1964, 1971) have adopted a much wider concept of the genus on one hand (including *Paragyrodon*, *Boletinus*, and apparently *Gyrodon*) while on the other hand, transferring all those species (including *S. aeruginascens*, *S. weaverae* with glandular dots on the stipe) with reddish to vinaceous, vinaceous-brown to purplish brown to lilac-drab or grayish brown spore print (after dehydration) in a genus *Fuscoboletinus*. Neither the introduction of *Boletinus cavipes* in *Suillus* nor the separation of *Fuscoboletinus* from *Suillus* has been accepted by modern specialists (Snell, Dick, Singer, Watling, Moser, Bresinsky) since, in that scheme, all natural groups (*Boletinus*, and the sections of *Suillus*) are split up according to the color of the dehydrated spore mass. Bresinsky & Rennschmid have shown that pigment analysis does not support an overruling importance of the spore color in the *Boletinus-Suillus* complex as far as the European species are concerned (1971, p. 317).

*Paragyrodon* and *Boletinus* are sharply separated from *Suillus* (see also under these genera). See also under "Limits" of the genera *Pulveroboletus* and *Chalciporus* (p. 768 and p. 771).

*State of knowledge:* The genus has been studied monographically by several authors, alone and in the complex of Boletaceae. 42 species are here definitely accepted and enumerated.

*Practical importance:* This genus is one of the most interesting with regard to its mycorrhiza relations which are rather constant and selective. It plays already an important rôle in forestry, especially *S. granulatus*, *S. placidus* and *S. plurans* since these have been used (and are in some places commercially produced and available) as inoculum for trees to be planted in regions outside the ectotroph area. Besides, there are several valuable edible fungi in this genus, some of them widely collected and sold in the markets in Europe, Asia, South America, and in Chile exported as dried mushrooms (Pichi loyo - *S. luteus*) as a by-product of pine plantations.

## SPECIES

Sect. 1. *SOLIDIPEDES* (Sing.) Sing. 1967. Pileus covered with non-gelatinous fibrils mostly forming scales; hypodermium sometimes becoming gelatinized in age;

veil mostly tending to gray: stipe without glandular dots. Pilangiocarpous (at least in *S. spectabilis*).

*Type species: S. pictus* (Peck) Smith & Thiers.

Subsection *Pictini* Sing. (1938 sub Boletino). Mostly under *Pinus* sp. or under *Abies*, *Picea*, *Pseudotsuga*; spore print (dehydrated) not with a reddish or grayish-purple tinge, fresh between "Antique bronze" and "oak" (M & P).

*Type species: S. pictus* (Peck) Smith & Thiers.

*S. pictus* (Peck) Smith & Thiers (Boletinus, Peck); *S. decipiens* (Berk. & Curt.) O. Kuntze (Boletinus, Peck); *S. amabilis* (Peck) Sing. (Boletus lakei Murr.; Ixocomus, Sing.; Suillus, Sing.\*).

*Gastroid conditions of Suillus decipiens* (see pl. 76,5), are of special interest for the systematist but, unfortunately, few collections have been made, and no living mycologist has collected fresh material of fertile gastroid carpophores. The dried specimens collected by R. Thaxter in Central Florida have been studied by the author. They are all smaller than the average size of *S. decipiens*. They do not open up in the way most Agaricales do, but remain closed and Gastromycete-like all through their development which evidently is endocarpous. Their shape is piriform; they have a columella (apex of the stipe) and labyrinthic loculi (hymenophore) confined to the lower side of the peridium (pileus) and producing spores which are of the same shape and the same size and color as those of the normal form of the *Suillus*, viz. 7-9.6 × 3-3.8 µm with the same thickness of the wall, and they originate on basidia which are in no way different from these of the "pseudoangiocarpous" form. The spores are consequently heterotropic and axially asymmetric as all other spores of Agaricales are, and not as the majority of the spores of Gastromycetes. This is the main difference between this form and the genus *Truncocolumella*. The existence of these gastroid forms is considered by C. Dodge, the author, and others as an additional evidence of the affinity of the boletes and the Gastromycetes, more precisely the group in which *Truncocolumella* belongs, i.e. the Gastroboletaceae. It would be very interesting to show experimentally what precisely causes the aberrant carpophores to remain gastroid. This may throw some more light on the phylogenetic implications of this subject. Could it be that these carpophores were subjected to dry conditions while still in the primordial stage? Or should we rather think of them as an independent unit of a similar status as now recognized for *Gastroboletus* or *Macowanites*? Unless experimental work decides the issue, or more detailed observations are available in Florida - we cannot be certain.

Subsection *Spectabilis* (Sing.) Sing. Generally associated with *Larix*; spore print (dehydrated) with purplish tinge.

*Type species: S. spectabilis* (Peck.) Sing.

*S. spectabilis* (Peck) O. Kuntze; *S. ochraceoroseus* (Snell) Sing.; perhaps also *Bole-*

\*See Singer, *Mycologia* 62: 590-596. 1970.

*tinus oxydabilis* Sing. in spite of the presence of a few clamps here and there in some specimens).

Sect. 2. *GLANDULOSI* Sing. in Sing., Snell & Dick (1963). Pileus, or both pileus and stipe viscid or glutinous, if fibrillose, fibrils imbedded in the gluten; hymenophore boletinoid, yellow to brown (not white to gray); spore print generally with a purplish hue (dehydrated); annulus present; tubes becoming spotted with dark dots when old (from fasciculate cystidia); mycorrhiza with conifers other than *Larix*. Otherwise like sect. 1 or 3.

*S. glandulosus* (Peck) Sing.; *S. sinuspaulianus* (Pomerleau & Smith) Sing.

Sect. 3. *LARIGNI* (Sing.) Sing. 1945. Annulus usually well developed; stipe without glandular dots; pileus not squamulose or squamose as in sect. 1 and *Boletinus*, but glabrous (except for occasional remnants of the veil) and viscid to glutinous; hymenophore either with wide (pores  $> 1$  mm), often boletinoid pores and then white to gray or yellow (and then becoming orange-rusty or gray in age) or small and not boletinoid and then yellow and remaining yellowish; spore print as in section 2 and then between "Cochin" and "burned umber" (Maerz & Paul) before dehydration, or more "snuff brown" to "fawn color" (Ridgway) or "bure" (M & P), or somewhat variable to cinnamon brownish or when fresh somewhat olive (in subsection *Leptosporini*); only a pulvinic pigment turning blue or violet in  $H_2SO_4$  present, rarely variegatic acid also present, variegatorubin and grevellin D absent or present, grevellin A, B, C present. Mycorrhiza with *Larix*, very exceptionally also with *Pinus* (?). Mixangiocarpous.

Type species: *Suillus grevillei* (Klotzsch) Sing.

Subsection *Megasporini* Sing. (1938, as subsection of *Ixocomus*) (*Fuscoboletinus* sect. *Griselli* A.H. Smith 1965). Pores wider or as wide as 1 mm; hymenophore more or less boletinoid, white to gray, more rarely yellow and becoming duller or gray, aside from (or instead in some cases?) grevellin also pulvinicacid derivatives present.

Type species: *S. aeruginascens* (Secr.) Snell.

*S. aeruginascens* (Secr.) Snell with var. *aeruginascens* and var. *bresadolae* (Quél. in Bres.) Moser in Gams; *S. nueschii* Sing.; *S. tridentinus* (Bres.) Sing.; apparently also (if autonomous) *Boletus serotinus* Frost and *B. grisellus* Peck and possibly *S. ponderosus* Smith & Thiers and *S. imitatus* Smith & Thiers.

Subsection *Leptoporini* (Sing. sub. *Ixocomo* 1938; sub. *Suillo* 1945). Pores small to medium wide; hymenophore yellow, sometimes discoloring by autoxidation (but not becoming gray) or orange rusty at maturity, very rarely grayish, not or not strongly boletinoid; aside from grevellin A, B, C also tridentin, but no xerocomic acids present.

Type species: *I. elegans* (Schum. sensu Fr.) Sing. = *S. grevillei* (Klotzsch) Sing.

*S. grevillei* (Klotzsch) Sing.; apparently also *S. jacuticus* (Sing.) Sing., *S. proximus* Smith & Thiers, and *S. hololeucus* Pantidou.

Sect. 4. *SUILLUS* (*Granulati* Sing. 1938). Stipe with glandular dots (these often concolorous with the ground color of the stipe when the specimens are young, rarely all through development, consisting of (oleo-)dermatocystidia arranged in clusters or fascicles, mostly incrusted with resinous masses which may become so abundant that the stipe is covered by confluent sheets of dark sticky matter); veil present (and then appendiculate on the margin, or forming an annulus) or absent; if an annulus is present, this may be broadly sheathing the stipe or flare out, usually membranous, rarely gelatinous-glutinous (and then strictly with pine-mycorrhiza and context not bluing), but often viscid on the outside; hymenophore rarely strictly boletinoid although the pores may be somewhat radially elongated and wide; spore print color variable. Development pilangiocarpous in the evelate forms, mixangiocarpous in the annulate forms. Mycorrhiza with *Pinus*, rarely with other Pinaceae, not with *Larix*.

Type species: *S. luteus* (L. ex Fr.) S.F. Gray.

Subsection *Latiporini* Sing. (1938). Fresh spore print cinnamon without an olive tinge; pores wide, somewhat boletinoid, wider than 1 mm when quite mature. Variegatic acid and variegatorubin absent (maybe present in mycelium in cultures according to Besl & Bresinsky).

Type species: *S. flavidus* (Fr.) Sing.

*S. flavidus* (Fr.) Sing.; *S. sibiricus* (Sing.); *S. umbonatus* Dick & Snell; *S. punctatipes* (Snell & Dick) Smith & Thiers; *S. americanus* (Peck) Snell; obviously also *Fusco-boletinus weaverae* Smith & Shaffer.

Subsect. *Suillus* (Angustiporini Sing. 1938). Spore print cinnamon; pores usually smaller than 1 mm wide, rarely reaching 1 mm in fully mature specimens. Variegatic acid and variegatorubin absent.

Type species: *S. luteus* (L. ex Fr.) S.F. Gray.

*S. subluteus* (Peck) Snell apud Slipp & Snell; *S. cothurnatus* Sing. with two seasonally dimorphous subspecies: spp. *clothurnatus* and spp. *hiemalis* Sing.; *S. luteus* (L. ex Fr.) S.F. Gray; *S. placidus* (Bon.) Sing. (*Boletus albus* Peck; *B. capricollensis* Henn.); *S. granulatus* (L. ex Fr.) O. Kuntze (with two mycoecotypes: ssp. *granulatus* and ssp. *snelli* Sing.); *S. leptopus* (Pers.) Marchand; *S. bellinii* (Inz.) Watling; *S. pseudobrevipes* Smith & Thiers; *S. albipes* (Peck) Sing.; *S. acerbus* Smith & Thiers; *S. brevipes* (Peck) Kuntze; *S. collinitus* (Fr.) O. Kuntze (*S. fluryi* Huijsm.); *S. brunnescens* Smith & Thiers; *S. pungens* Thiers & Smith in Smith & Thiers; *S. pseudogranulatus* (Murr.) Smith & Thiers (*Boletus*, Murr.); *S. brevipes* var. *pseudogranulatus* (Murr.) Sing.; *S. chiapasensis* Sing.; *S. acidus* (Peck) Sing.; obviously also *S. subalutaceus* (Smith & Thiers) Smith & Thiers; *S. intermedius* (Smith & Thiers) Smith & Thiers; *S. glandulosipes* Thiers & Smith in Smith & Thiers; *S. lutescens* Smith & Thiers; *S. pallidiceps* Smith & Thiers.

Subsection *Hirtellini* Sing. (1945). Spore print before dehydration with a distinct olive tinge; pore width rather variable, often intermediate between that of the preceding two subsections; pileus often fibrillose-rough to squamulose (innately so). Variegatic acid and variegatorubin present (at least in *S. plorans*).

*Type species: S. hirtellus* (Peck) O. Kuntze.

*S. subaureus* (Peck) Snell (sensu Smith & Thiers); *S. plorans* (Rolland) Sing.; *S. ruber* Sing. & Snipe apud Sing.; *S. tomentosus* (Kauffm.) Sing.; *S. punctipes* (Peck) Sing.; *S. hirtellus* (Peck) O. Kuntze with two subspecies, ssp. *cheimonophilus* Sing. and ssp. *thermophilus* Sing. aside from the type subspecies (northern): ssp. *hirtellus*; probably here *S. chiapensis* Sing.

*Note:* Subsection *Hirtellini* may be elevated to sectional rank once all species have been submitted to pigment analysis.

Sect. 5. *FUNGOSI* (Smotlacha) Sing. (1965) (*Bovini* Sing. 1938 sub *Ixocomo*). Stipe without glandular dots; veil absent; spore print (fresh) with a slight olive tinge as in subsection *Hirtellini* of sect. *Suillus*; variegatic acid and variegatorubin present; development pilangiocarpous or gymnocarpous. Mycorrhiza with *Pinus*, rarely with other Pinaceae, not with *Larix*.

*Type species: S. variegatus* (Sw. ex Fr.) O. Kuntze.

Subsect. *Euryporini* (Sing.) Sing. (1945, 1951). Pores wide (more than 1 mm in diameter); pileus not fibrillose-squamulose; context reacting more indistinctly (inconstantly and fugaciously sordid lilac-reddish) with ammonia; development pilangiocarpous.

*Type and only known species: S. bovinus* (L. ex Fr.) O. Kuntze with var. *viridicæ-rulescens* (Pearson) Sing.

Subsection *Stenosporinae* (Sing.) Sing. (1945, 1951). Pores small to medium wide; pileus fibrillose-squamulose; context reacting mor indistinctly (inconstantly and fugaciously sordid-lilac-reddish) with ammonia; development pilangiocarpous.

*Type species: S. variegatus* (Se. ex Fr.) Kuntze.

*S. variegatus* (Sw. ex Fr.) O. Kuntze.

#### Subfamily Xerocomoideae Sing.

*Farlowia* 2: 279. 1945.

*Type genus: Xerocomus* Quél.

*Characters:* Hyphae not clamped or very rarely showing very few clamp connections (and then the hymenophore usually lamellate); spores fusoid-subcylindric (Pl. 76, 11), smooth (light microscope; but several species very slightly striate or rugulose in SEM according to Pegler & Young 1981), sometimes rather short, mostly olivaceous brown in print; pileus subtomentose or tomentose in dry weather, often slightly to distinctly viscid in wet weather; hymenophore lamellate (often with venose anastomoses), or tubulose and then the pores more often wide (diameter larger than 1 mm) or medium sized, often irregular and compound, but rarely of a true boletinoid type, adnate or decurrent, more rarely with a very slight depression around the apex of the stipe; cystidia (Pl. 76, 12) hyaline or melleous, often hyaline or melleous-incrusted; hymenophoral trama bilateral of the *Phylloporus* type, rarely of a structure somewhat intermediate between the *Boletus*-type and the *Phylloporus*-type

(*Xerocomus*, sect. *Pseudoboleti*, less so in sect. *Moravici*); stipe solid, cylindric or subcylindric, rarely ventricose, without a veil, rarely (in *Xerocomus*, sect. *Brasilien-ses*) with a dry, cortinoid, fugacious veil, without glandular dots, never viscid or sticky. Ectomycorrhizal or not. On the earth, on wood, on gastromycetes, and on anthills.

#### KEY TO THE GENERA

- |                             |                                  |
|-----------------------------|----------------------------------|
| A. Hymenophore lamellate.   | 211. <i>Phylloporus</i> , p. 758 |
| A. Hymenophore tubulose.    | 212. <i>Xerocomus</i> , p. 760   |
| B. Without setoid cystidia. | 213. <i>Tubosaeta</i> , p. 764   |
| B. With setoid cystidia.    |                                  |

### 211. PHYLLOPORUS Quél.

*Flore Mycol.*, p. 409. 1888.

*Type species:* *P. pelletieri* (Lév. apud Crouan) Quél. [= *P. rhodoxanthus* (Schw.) Bres. ssp. *europaeus* Sing.]

Syn.: *Gymnogomphus* Fayod; *Prodr.*, *Ann. Sc. Not. Bot.* VII9: 385. 1889.

*Characters:* All characters as in the subfamily but the hymenophore lamellate (with anastomoses in most cases); the cuticle of the pileus when young and fresh always turning vivid blue with ammoniacal vapors except in sect. 2; hymenophoral trama always with a lateral stratum consisting of hyphae touching each other (not very loosely arranged) and moderately strongly divergent, not or not much paler colored than the mediostratum, i.e. constantly of the *Phylloporus*-type and never intermediate between the latter and the *Boletus*-type. On the ground, more rarely on decayed wood under trees; obligatorily ectomycorrhizal at least in sect. *Phylloporus*. Pl. 76, 11-12.

*Development of the carpophores:* Unknown.

*Area:* Of almost general occurrence in the ectotroph area, including the oak woods of Central America south to Colombia; and reaching (with *Alnus*) northern Argentina, also in Amazonia, Tropical Africa and Southern as well as Eastern Asia.

*Limits:* The ammonia-reaction is characteristic for all well-known (in fresh condition) species of sect. *Phylloporus*. Even though some African and South American forms show an occasional transition toward tubular configuration (having often strongly developed and high anastomoses between the lamellae), it is still easy to distinguish a basically lamellar and a basically tubular type. In all particulars, *Phyllo-*

*porus* is so close to *Xerocomus* that it is hardly understandable why some authors relegate this genus to another family (Paxillaceae). *Phylloporus* differs from all Paxillaceae in the spore print color and/or the absence of clamp connections. No blue ammonia reaction in ectomycorrhizal Paxilli has ever been observed. On the other hand *Phylloporus* never develops an annulus. In addition chemotaxonomic studies by Bresinsky & Rennschmid (1971) show that "the recently again controversial position of *Phylloporus* (compare the opinion of Smith and Thiers 1971 which differs from Singer's 1962) has been surely cleared up by the characters of the pigments which turned out to indicate no differences with regard to the Xerocomoidae, but considerable ones concerning the Paxillaceae".

It may be instructive to put side by side two opinions - both extreme - about the position of *Phylloporus*:

"We place *Phylloporus* in the Paxillaceae, following Watling" (Smith & Thiers, *Bol. Mich.* p. 26. 1971).

"Rappelons que ces deux genres [*Phylloporus* and *Xerocomus*] sont extrêmement voisins et que leur maintien ne se justifie guère que pour des raisons pratiques" (Heinemann, *Flore Iconographique Champ. Congo* p. 296. 1935-71).

The species entering *Gymnogomphus* Fayod which we indicate as a synonym are neither published nor precisely identifiable. The short description fits both *Chroogomphus* (and perhaps *Gomphidius*) and *Phylloporus*. This genus is based on two species from Japan (collection Döderlein) which cannot be found in any of the likely herbaria consulted. However, a search in the Fayod herbarium (G) produced a few documents which throw some light on the genus as understood by Fayod. In the first place, there is an excellent plate of a fungus painted by Fayod and called *Gymnogomphus helveticus* Fayod [ined.]. This is easily identified as *Chroogomphus helveticus* (Sing.) Moser in Gams. Furthermore, sketches and notes were found with the help of Dr. O. Monthoux. This material (G) obviously refers to some material in alcohol, since lost: *G. doederleini* [Fayod, ined.] and *G. japonicus* [Fayod, ined.]. Of these, the former, particularly because of spore size, habit, and fascicular growth, is undoubtedly a *Phylloporus* sect. *Phylloporus* spec.; the latter, because of spore size, habit (with umbo) and probable viscosity is gomphidiaceous, and, with reference to Fayod's *G. helveticus*, probably *Chroogomphus*. Since we cannot be absolutely certain about the genus because of the absence of specimens and the lack of an indication of the locality in Japan, which makes it impossible to obtain a topotype, *G. doederleini* is here considered as the holotype, and the genus is placed in synonymy with *Phylloporus*.

*State of knowledge:* After our own (Singer & Gomez, *Brenesia* 22: 163-182, 1984), and Corner's (1970) and Heinemann's (1954, 1960) studies, the general scope and the knowledge of many species in *Phylloporus* has progressed much as compared to the state of knowledge at the time the genus was first proposed. I recognize 16 species known to me personally, adding below some of those keyed out by Corner, *Nov. Hedw.* 20: 793. 1970.

*Practical importance:* Some or all species of *Phylloporus* are edible but, neither in

culinary value nor in marketing possibilities, very attractive and, in addition, in most countries rather rare. Most or probably all species are ectotroph formers, and may have some value in forestry in the future.

## SPECIES

Sect. *PHYLLOPORUS*. Spore print brown to olive without a purple shade; NH<sub>3</sub> and NH<sub>4</sub>OH staining the surface of the fresh pileus blue.

*Type species:* Same as that of the genus.

*P. rhodoxanthus* (Schwein.) Bres. with ssp. *rhodoxanthus* and ssp. *europaeus* Sing.; *P. phaeoxanthus* Sing. & Gomez; *P. centroamericanus* Sing. & Gomez; *P. bellus* (Mass.) Corner; *P. leucomycelinus* (Sing.) ex Sing.; *P. caballeroi* Sing.; *P. purpurellus* Sing.; *P. sulcatus* (Pat.) Gilbert; *P. foliiporus* (Murr.). Sing. (*Gomphidius foliiporus* Murr., *Mycologia* 35: 432. 1943); *P. hyperion* (Cooke & Mass.) Sing.; *P. pinguis* (Hook. f.) Sing.; *P. sulphureus* (Berk.) Sing.; *P. depressus* Heinemann and obviously other tropical-African species; obviously *P. infundibuliformis* (Cleland) Sing.; *P. tunicatus* Corner, *P. orientalis* Corner and other tropical Asiatic species; *P. luxiensis* M. Zang and *P. scabrosus* M. Zang (unless identical with one of the above species).

The species enumerated above turn blue or are unchanging in hymenophore and context. Species which are, instead, reddening and/or blackening may require a special subsection: *P. bogoriensis* Höhn. (studied by me as *P. rhodoxanthus* ssp. *bogoriensis*, but according to Corner (1970) macroscopically quite different) and apparently *P. rufescens* Corner.

Species evidently belonging in *Phylloporus* but spore print color and NH<sub>3</sub> reaction unknown: *P. viridis* (Berk.) Sing.

Sect. *MANAUSENES* Sing. (1978). Spore print "sandalwood" to "Leather br." or "marron glace" in thin, "Vandyke br" to "Cochin" (M & P) in thick layer, never (fresh) with an olive tinge; NH<sub>3</sub> and NH<sub>4</sub>OH on the surface of the pileus (fresh) not bluing.

*Type species:* *P. manausensis* Sing.

*P. manausensis* Sing.

## 212. XEROCOMUS Quél.

In Mougeot & Ferry, Champ. in Louis, Dep. Vosg., *Fl. Vosg.*, p. 477. 1887; *Flore Mycol.*, p. 417. 1888. nom. conserv.

*Type species:* *X. subtomentosus* (L. ex Fr.) Quél.

Syn.: *Xerocomopsis* Reichert, *Palest. Journ. Bot. Reh.* Ser. 3: 229. 1940.

**Characters:** Pileus more or less tomentose or subtomentose, frequently with at least a fragmentary trichodermium or palisade; hymenophore not lamellate, occasionally subboletinoid but never truly boletinoid, most frequently with rather wide and angular pores, adnate, often with a decurrent tooth, or arcuate-decurrent, more rarely becoming depressed around the stipe and then usually the radial walls of the tubes forming a sublamellate ring around the apex of the stipe, not free, but sometimes separating in age; spores variable in size, subcylindric to subfusoid, or ellipsoid-oblong to ellipsoid-subclavate, sometimes almost ellipsoid-ovoid and rather short; always olivaceous brown in print (Pl. 52, 1, 2, 4, 8); hymenophoral trama of the *Phylloporus*-type (*Phylloporus*-subtype of the bilateral type), i.e. lateral stratum consisting of moderately diverging and not very loosely arranged hyphae, not much or not at all paler than the mediostratum, in sect. *Pseudoboleti* the structure of the trama intermediate between the *Phylloporus*-subtype and the *Boletus*-subtype (hyphae of the lateral stratum distinctly divergent, looser than in the mediostratum but still mostly touching each other, hyphae of the mediostratum slightly subparallel-subinterwoven and slightly colored, deeper than the practically hyaline lateral stratum); cystidia medium-sized to rather large, not strikingly incrusted, or not incrusted at all, not in fascicles; setuloid cystidia none; stipe usually cylindric, or subequal and comparatively rather thin, more rarely assuming some other shape, and very rarely ventricose-bulbous as in *Boletus*, sometimes with an ocher-brown to chestnut colored, coarse network at the apex of the stipe, never finely reticulated as in *Boletus*; veil sometimes present, cortinoid, fugacious, or more frequently none; yellow pulverulence none; glutinous covering of stipe or pileus absent; context unchanging or changing color, often bluing in certain portions; all hyphae without clamp connections. On soil, humus, very decayed wood, anthills, and carpophores of Sclerotermatinae, in the woods, and in gardens near trees.

**Development of the carpophores:** Hypovelangiocarpous (paravelangiocarpous) in *X. parasiticus* and probably *X. radicicola*, gymnocarpous in *X. subtomentosus* and apparently the majority of the species (Reijnders), certainly *X. badius* (Pantidou) and *X. illudens* (Pantidou), generally stipitocarpous but in *X. parasiticus* paleo-stipitocarpous.

**Area:** Some species tropical, the majority temperate, but in the South American temperate (*Nothofagus*-)zone absent or very rare.

**Limits:** The genus *Xerocomus* is closest to *Phylloporus* (see there). It differs from *Chalciporus* in the combination of reddish hymenophore and yellow basal mycelium never existent while it is constant in *Chalciporus*. It differs from *Pulveroboletus* in the absence of a pulverulence (yellow or green) and of a viscid coating of the stipe, never cartilaginous or hollow stipe and not decidedly *Boletus*-like hymenophoral trama; besides *Pulveroboletus* always lacks even a fleeting dark blue reaction with ammonia on the surface of the pileus. Arcuate hymenophoral surface, strictly lignicolous or graminicolous habit, a glutinous or bright colored veil, ferruginous spore print, and a tendency of the dried pileus to develop a detersile external layer indicate *Pulveroboletus*. The sections and species of *Boletus* differ sharply in appearance with the exception of sect. *Subpruinosi*.

The difference between sect. *Subpruinosi* and *Xerocomus* is fundamentally based on the difference in the structure of the hymenophoral trama. Those species of *Xerocomus* where a somewhat intermediate structure is observed, differ from sect. *Subpruinosi* of *Boletus* further by (1) never showing an epithelium as epicutis, (2) never having bright and deep yellow nor red pores, unless the context and hymenophore are both not bluing by autoxidation, (3) by being never smaller than 10 mm, (4) by not being obligatorily ectomycorrhizal. If, in addition to the characters emphasized in the key and the generic descriptions, these details are considered, one should arrive at a fairly natural and practically satisfactory hiatus between the two genera (and subfamilies). It is not claimed here that these limits are fully satisfactory including all species that still may be found or which have not come to the attention of the author until now. This is so because some species are still incompletely known, partially as far as some of the important chemical or anatomical characters are concerned. There is, however, hope that chemotaxonomical studies, particularly pigment analysis on a larger number of species, including the tropical ones, will in the end establish or improve the delimitation of *Xerocomus*. In the meantime, with the evidence showing that the extremes of Xerocomoideae and Boletoideae are - in many important characters - as far apart as any boletaceous groups could be, I cannot accept a solution by which *Phylloporus rhodoxanthus* and *Boletus edulis* should be in a single genus *Boletus* unless we wish to return to 1821 when all Boletaceae were *Boletus*. More so because those authors who combine Xerocomoideae and Boletoideae, or *Boletus* and *Xerocomus* into a single genus, will inevitably come up with a subgenus *Xerocomus* or some other taxon which takes the place of *Xerocomus* yet if *Xerocomus* actually were not separated from *Boletus* by a hiatus, or if it were an artificial grouping, it would be just as artificial if recognized on a slightly lower level.

*State of knowledge:* There are now 27 fully known species of *Xerocomus* in the sense that they can be introduced in the various infrageneric taxa recognized in *Xerocomus*.

*Practical importance:* It is certain that several species of *Xerocomus* are not obligatorily ectomycorrhizal - *X. parasiticus* is merely parasitic on an ectomycorrhizal Gastromycete -, even some of those that obviously have a wide range of mycorrhizal symbionts and are only facultative ectotroph-formers. This physiological-ecological intermediate position between such non-mycorrhizal genera as *Meiorganum* and the constantly obligatorily mycorrhizal genera like *Boletus* or *Suillus* is shared with such genera as *Pulveroboletus* and perhaps *Chalciporus*. The fungus which forms mycorrhiza at the same time with conifers and with *Monotropa* is obviously also a *Xerocomus*. Some species are, however, definitely ectomycorrhizal (e. gr. with *Shorea* in India). Many are edible but they are not as valuable market fungi as are the edible species of *Boletus*.

## SPECIES

Sect. 1. *PSEUDOPHYLLOPORI* Sing. (1945). Ammonia reaction bright and rich blue on the young, fresh pilei ("porcelain blue" or "dusky green blue" of Ridgway).

Type species: *X. illudens* (Peck) Sing.

*X. hypoxanthus* Sing.; *X. pseudoboletinus* (Murr.) Sing. (*Ceriomyces*, Murr.); *X. carnosus* (Rostk.) Sing. (*Boletus carnosus* Rostk. in Sturm, *Deutschl. Fl.* III.5, l. 14. 1844; *B. subtomentosus* var. *punctipes* Martin; ? *B. hoseneae* Smith & Thiers) with var. *pini-caribaeae* Sing.; *X. hemixanthus* Sing.; *X. illudens* (Peck) Sing. (with ssp. *xanthomycelinus* Sing.); *X. lanatus* (Rostk.) Sing. (*Boletus*, Rostk.; *Boletus leguei* Boudier); *X. spadiceus* (Fr.) Quél. (sensu Fr., Sing., Smith & Thiers, non Watling); *X. flavus* Sing. & Kuthan; *X. amazonicus* Sing.

Sect. 2. *XEROCOMUS* (*Subtomentosi* (Fr.) Sing. 1942). Ammonia reaction not blue in young, fresh material but either indistinctly darkening, livid, or for seconds bluish-black, or else negative, eventually mostly raching a brown or chestnut color; mycelium never parasitic on the carpophore of Gasteromycetes; trama truly and consistently of the *Phylloporus*-type; pileus not tomentose and viscid at the same time, in fact rarely viscid at all in the well known species. Gymnocarpous.

Type species: *X. subtomentosus* (L. ex Fr.) Quél.

*X. subtomentosus* (L. ex Fr.) Quél.; *X. chrysenteron* (Bull. ex St-Amans) Quél.; *X. truncatus* Sing. Snell & Dick; *X. bakshii* Sing. & Singh; *X. junghuhnii* (Höhn) Sing.; *B. tomentosulus* Smith & Thiers; *B. subparvulus* Smith & Thiers; *X. lentistipitatus* (Stevenson) McNabb; *X. dryophilus* (Thiers) Sing\*; *X. campinaranae* Sing. in Sing., Araujo & Ivory; *X. chapinii* Sing. in Sing., Araujo & Ivory; *X. inundabilis* Sing. in Sing., Araujo & Ivory; *X. globuliger* Sing. in Sing., Araujo & Ivory; obviously also *X. nothofagi* McNabb (with red pores).

Sect. 3. *PARASITICI* Sing. (1942). As in the preceding section but growing parasitically on the carpophores of *Scleroderma* (perhaps occasionally also on other fungi); context not or scarcely bluing; trama of the *Phylloporus* subtype. Hypo-(para)-velangiocarpous.

*X. parasiticus* (Bull. ex Fr.) Quél. (*Boletus*, Bull. ex Fr.); perhaps also *X. astraeicola* Imazeki.\*\*

Sect. 4. *BRASILIENSES* Sing. (1945). Pileus tomentose and often viscid at the same time; pores initially rather small, then becoming large or, comparatively, gigantic; spores small (6-9.3 × 2.8-4.2 µm); otherwise as in the *Subtomentosi*, but context unchanging (not bluing). Development apparently (always?) as in sect. 3. If parasitic, not on Gasteromycetes but on Angiosperm roots. Tropical.

Type species: *X. brasiliensis* (Rick) Sing.

\*c.n. (*Boletus dryophilus* Thiers, *California Mushrooms*, p. 82. 1975).

\*\*But hymenophoral trama of the *Boletus*-type according to Hongo and therefore possibly rather to Boletoideae.

*X. brasiliensis* (Rick) Sing. (*Boletus*, Rick); *indicus* Sing.; *X. microsporus* Sing. & Grinling; *X. alliaceus* (Beeli) Heinemann; *X. radicicola* Sing. & Araujo.

Sect. 5. *MORAVICI* Herink (1964). Much like the preceding section, but spores medium sized (8-13 × 3.5-5.5 µm). This section differs from sect. 2. by unchanging hymenophore and context (not bluing). Tropical and temperate species.

*X. moravicus* (Vacek) Herink (*X. tumidus* (Fr.) Gilbert sensu Peltereau non Fr.); *X. scrobiculatus* Sing. in Sing., Araujo & Ivory; *X. phaeocephalus* (Pat. & Baker) Sing. in Sing., Araujo & Ivory, obviously also *B. leonis* Reid (*X. boudieri* Sing.; *B. leoninus* Pers. sensu Boud. non Pers. nec Krombh. non *Boletus boudieri* Quél.), perhaps *B. roxanae* Frost.

Sect. 6. *PSEUDOBOLETI* Sing. (1945). Pileus somewhat viscid or dry and tomentose, depending on the amount of humidity adsorbed, or granulose-floccose; trama structure intermediate between the *Phylloporus*-subtype and the *Boletus*-subtype; ammonia provoking a blackish blue reaction on fresh and young specimens (surface of the pileus), but this reaction disappears very rapidly. Pores and context bluing by autoxidation; spores rather large (11.5-18.5(24) × 4-5.7 µm); pores medium wide, rather pale colored with a greenish tinge or pale yellowish. On the ground in woods (coniferous or frondose), not obligatorily ectomycorrhizal.

Type species: *X. badius* (Fr.) Kühner ex Gilbert.

*X. badius* (Fr.) Kühner ex Gilbert; possibly also *B. glabellus* Peck, *B. albocarneus* (Peck) Peck; *B. badiorufus* Heim; *B. tumidus* Fr.; *B. vaccinus* Fr.; *B. stejskalii* Bres. ex Stejskal (but their relation to *X. badius* requires additional studies; in the case of the last three they are merely thick-stemmed forms of *X. badius*).

Note: Section 6 may be just as well placed in *Boletus* since it is obviously intermediate between the two genera. However, a number of facts, now known or recently appreciated, are in favor of maintaining *X. badius* in *Xerocomus* where Kühner, Gilbert, Moser, and Watling place it. These are the color (uncommonly pale for xerocomoid Boleti) of the hymenophore, and the evidently not obligatory ectomycorrhiza since the mycelium of *X. badius* is frequently not connected with the trees near which it grows; this fungus is often collected on rotten stumps and conifer cones.

## 213. TUBOSAETA Horak

*Bull. Soc. Bot. Suisse* 77: 362. 1967.

Syn.: *Setogyroporus* Heinemann & Rammeloo, *Bull. Jard. Bot. Belg.* 52: 481. 1982.

Type species: *Boletochaete brunneosetosa* Sing.

Characters: Much like *Xerocomus*, but setoid cystidia present, these ± pigmented, conspicuous.

Development of the carpophores: Probably gymnocarpous (Pegler).

**Area:** Palaeotropical.

**Limits:** This genus seems to be sharply different from most Boletaceae by the setoid cystidia (sclerocystidia\*).

**State of knowledge:** Four species are now fully known.

**Practical importance:** The association of *T. calocystis* with *Paramacrolobium* suggests that at least this species is ectotrophically mycorrhizal with leguminous trees.

## SPECIES

*T. brunneosetosa* (Sing.) Horak; *T. goossensiae* (Beeli) Horak; *T. calocystis* (Heinemann & Goossens) Horak; obviously also *Boletus mirans* Corner.

### Subfamily Boletoideae

**Type genus:** *Boletus* Dill ex Fr. em. Sing. (1947).

**Characters:** Pileus viscid or dry; stipe equal or ventricose-bulbous, viscid or dry; veil present or absent; if present, either pulverulent and yellow or orange-latericious or green, or else entirely glutinous; clamp connections always constantly and completely absent; glandulae none; hymenophoral trama always of the *Boletus*-subtype excepting a few species of *Pulveroboletus* (where, however, either a veil is present, or the hymenophore is ± decurrent with an arcuate surface); lateral stratum otherwise consisting of loosely (not touching each other) arranged hyphae which are strongly divergent, mostly distinctly arcuate-recurred hyphae which are much paler than the mediostratum, mostly hyaline, the mediostratum rarely also subhyaline; hymenophore never distinctly boletinoid, and only exceptionally lamellar (in rare aberrant forms), usually somewhat to strongly depressed around the stipe. Ectomycorrhiza mostly formed (but not always in several genera) and obligatory in all species of *Boletus*, *Xanthoconium*, *Leccinum*, *Porphyrellus*, and *Tylopilus*.

### KEY TO THE GENERA

- A. Fungi with at least one of the following characters: (a) hymenophore at maturity flat or concave and tubes decurrent or adnate, arcuate (b) tubes all through dull, cinnamon red, carmine to wine red, pink, (c) veil present or stipe with a viscid or gelatinized outer layer, or cartilaginous and hollow and slender (5-10 mm). In case (a) applies, the spores are smooth; if (b) applies, the basal mycelium is constantly at least in part yellow; if (c) applies the spores are smooth.
- B. Veil present.
  - C. Veil yellow, green or orange (see "E" below).
  - C. Veil colorless or white.

\*Some additional species have been compared with *Tubosaeta* by Corner (1972) viz. *Boletus hastulifer* Corner, *B. aculifer* Corner, *B. calocystides* Corner. It is somewhat doubtful whether they can be presented into *Tubosaeta* since the cystidia are colorless. Type studies are necessary. *B. craspedius* Mass. also mentioned by Corner in this connection is undoubtedly a *Boletus*, sect. *Luridi*.

D. Veil dry; spore print purplish.

221. *Veloporphyrrellus*, p. 791

D. Veil not dry but glutinous, or else spore print olive, brown, or ferruginous.

E. Stipe scabrous, solid (see "G" below: *Leccinum*).

E. Stipe not scabrous (see "K" below: *Pulveroboletus*).

B. Veil absent (the projecting margin of some Leccina is not considered to be a veil).

F. Hymenophore all through dull cinnamon red, carmine to wine red or pink; basal mycelium at least partially bright yellow; stipe always evelate, solid, elements of its cortical layer never gelatinized; taste, if not mild,  $\pm$  acrid-peppery. 214. *Chalciporus*, p. 767

F. Hymenophore differently colored and/or not with yellow basal mycelium; pores often a bright deep yellow even in dried condition; taste not peppery but often salty; stipe often hollow and/or glutinous, or pulverulent (see "K" below).

A. Fungi not combining the characteristics indicated under (a), (b) or (c) above or spores ornamented; basal mycelium yellow or white, or some other color.

G. Stipe with rough, furfuraceous to floccose-fibrous scabrosities which are pink or gray or fuliginous-blackish or at first concolorous with the ground color of the stipe but darkening later, rarely remaining yellow, sometimes connected with each other by a thin reticulation; mostly these scabrosities consisting of a conspicuous hyphal base which ends up in cystidial and/or basidial terminal cells, the dermatocystidia mostly of at least two different types, occasionally with some true clamps; spores usually large but quite smooth and narrow; context of base of stipe mostly fibrous and rather tough, often discolored (yellow, green, blue); stipe usually obclavate, more rarely subequal; ectomycorrhiza mostly with Salicales and Fagales, very rarely with Pinaceae or Ericaceae. 219. *Leccinum*, p. 785

G. Stipe without scabrosities, either smooth or reticulate or finely pustulate-pruiniate and the surface with bunches of dermatocystidia (with or without some basidia) arising directly from the longitudinal hyphae of the rind of the stipe, if stipe surface somewhat scabrous, spores either short or ornamented and not combining the characteristics enumerated above.

H. Spore print yellow, tawny yellow, or ferruginous-yellow and surfaces of the carpophores neither gelatinized nor glutinous; stipe quite glabrous and smooth; context unchanged; spores smooth; taste mild. 220. *Xanthoconium*, p. 790

H. Spore print not as indicated above or surfaces gelatinized or stipe not both glabrous and smooth.

I. Spore print olicaceous, olivaceous-brown or more rarely ferruginous.

J. Spores smooth (light microscope), generally also SEM - smooth.

K. Pileus and/or stipe with or without a yellow, orange or green detersile pulverulence or a viscid to glutinous covering which includes the surface of the stipe (and then cortical layer of stipe hyphae gelatinized), or else stipe cartilaginous and/or hollow, often fusoid, not bulbous; veil present or absent; mycelium ectomycorrhizal or not (even lignicolous in some species); hymenophoral trama bilateral of the *Boletus*-type, but sometimes even in young specimens transitorily of the *Phylloporus*-type; pores more often wide ( $> 1$  mm) than small; tubes sometimes arcuate-decurrent, sometimes adnexed to adnate, and often also distinctly depressed around the stipe (cf. *Xerocomus*, see p. 761). 215. *Pulveroboletus*, p. 770

K. Pileus without a yellow, orange or green pulverulence; stipe neither viscid nor glutinous; veil none; hymenophore consisting of tubes with a strictly *Boletus*-type hymenophoral trama, generally distinctly depressed around the stipe with the pores more often small (even stuffed when young) than wide; all species (obligatorily as far as known) ectomycorrhizal.

L. Spores extraordinarily large and when mature with rather thick walls, reaching  $20 \mu\text{m}$  or more in length; cystidial wall often slightly thickened; stipe often reticulate in part; margin of pileus often projecting (see "M" below).

L. Spores not in the range of  $17-25(33) \times 5.7-9-(12) \mu\text{m}$ , and rarely over  $18 \mu\text{m}$  long or over  $5.5 \mu\text{m}$  broad, with firm to only slightly thickened wall; cystidial wall generally thin. 216. *Boletus*, p. 775

J. Spores ornamented, often longitudinally striped or winged, melleous to brown, but olive to olivaceous brown and without a reddish tinge when seen in a fresh spore print; stipe and/or hymenophore and/or context distinctly yellow; pigments corresponding to those of the genus *Boletus* and/or *Xerocomus*, i.e. pulvinic acid derivatives present

in the carpophores; clamp connections present or absent; hymenophore lamellate or tubular.

M. Hymenophore tubular.

217. *Boletellus*, p. 780

M. Hymenophore lamellate.

218. *Phylloboletellus*, p. 784

I. Spore print pink, grayish-brownish-pink, cacao-brown, porphyry brown, porphyry red or rarely "cream buff" to "Isabella color" (Ridgway) and then context not unchanging, bitter.

N. Spores smooth (light microscope) (as far as known also under SEM); cystidia mostly with a pigmented and/or pseudoamyloid internal body, often pseudocystidioid, (if not cf. "D" above and "N" below) unless pileus viscid and/or scrobiculate and/or stipe thin and glutinous; veil generally absent.

O. Cystidia optically "empty", hyaline to yellowish, inamyloid; pileus scrobiculate or stipe viscid to glutinous or at least thin and cylindrical; thermophilous species, many tropical; hymenophoral trama (lateral stratum) so strongly gelatinized that in liquid medium the individual tubes separate; epicutis of pileus always becoming gelatinized.

225. *Fistulinella*, p. 796

O. Cystidia generally with pigmented or pseudoamyloid internal body (bodies) often pseudocystidioid (use dried or fresh material).

P. Pseudocystidia early becoming coscinoid; spores short ( $Q < 2$ ) and small  $5.5 - 6.7 \times 3.5 - 5 \mu\text{m}$ , very pale colored and inamyloid; taste bitter; hymenophore mostly adnate; carpophores of the slow-growing long-lived type (Corner). Palaeotropical.

224. *Boletochaete* Sing., p. 795

P. Cystidia not becoming coscinoid; spores either short or elongate, larger than indicated above.

Q. Spores rarely over  $15 \mu\text{m}$  long, over  $5 \mu\text{m}$  broad only is short (e. gr.  $9 - 12 \times 5 - 8 \mu\text{m}$ ) and the ammonia reaction with the fresh surface of the pileus blue, thin-walled if small, in print varying from light pink to between "wood brown", and "Argus brown" (Ridgway), more rarely between "cream buff" and "Isabella color" (Ridgway); KOH reacting or not with the context of the stipe but never reddish or purple; taste mild or bitter. Widespread.

223. *Tylopilus*, p. 793

Q. Spores as above or larger, but  $Q < 1.5$ ; ammonia reaction never blue; spore wall variable and often thicker in apical part; spore print near "warm sepia", "chestnut", or "benzo brown" (Ridgway); KOH typically reddish or purple on context which often turns blue or black on injury. North temperate.

222. *Porphyrellus*, p. 792

N. Spores ornamented; cystidia not with a pigmented inside body nor partly pseudoamyloid, not pseudocystidioid, not coscinoid; veil present or absent; stipe dry or glutinous.

226. *Austroboletus*, p. 798

## 214. CHALCIPORUS Bat.

*Bolets*, p. 19. 1908.

Type species: *Boletus piperatus* Bull. ex Fr.

Syn.: *Rubinoboletus* Pilát & Dermek, Česk. Myk. 23: 81. 1969.

**Characters:** Hymenophore tubular, rarely and exceptionally lamellate, pores concolorous with the tube-interior, dull red, ochre-red, reddish cinnamon, carmine, wine-red, pink or salmon pink, rarely a dull ochre-brown (and often becoming so in age), rather small to rather wide, usually not more than 1 mm broad, depressed around the stipe or adnate or even subdecurrent, but not arcuate; stipe without dark or concolorous asperulations (as in *Leccinum*) and not reticulate, subequal or at least not broad and bulbous-ventricose, not viscid, not hollow; veil none; basal

mycelial tomentum at least in part bright yellow; context white to ocher or rarely somewhat pinkish, sometimes bluing; spores either elongated or short ellipsoid (Pl. 52,7), pale melleous to brown NH<sub>4</sub>OH; spore print brown, e. gr. "sayal brown" (Ridgway) or between "Mohawk" and "burnt umber" when fresh, about "snuff brown" (Ridgway) when dried, typically without a discernible olive tinge when fresh; cystidia generally rather conspicuous, often covered by a resinaceous encrustation but the hyaline wall mostly thin, in one species wall thickened (according to Corner); hyphae without clamp connections; hymenophoral trama often wine red in the mediostratum, generally of the *Boletus*-type, but sometimes during a considerable period of the *Phylloporus*-type and eventually often less distinctly bilateral; pileus glabrous to somewhat fibrillose-subtomentose spotted or finely flocculose, with some degree of gelatinization in the cuticular layer (below the superficial fibrils or floccons), the epicutis often fragmentary and its trichodermium often soon applanate or fugacious; taste mild, bitterish or peppery (acrid); ectomycorrhizal but not strictly specialized and not always obligatorily symbiotic. Pigments: Variegatic acid, variegatorubin, atrotomentinic acid, xerocomic acid (all present in the type species).

*Development of the carpophores:* Gymnocalypous and stipitocarpous (McLaughlin, *Mycologia* 56: 136-138. 1964; see also 62: 307-331. 1970).

*Area:* Temperate and tropical zones of both hemispheres.

*Limits:* The genus *Chalciporus* was formerly thought to be a section (*Piperati*) of *Suillus*. However, when species with ellipsoid spores and non-coniferous root-associations have become better known, it became obvious that this very natural group is better placed as a separate genus in the Boletoideae, close to *Pulveroboletus*. The combination of several strictly correlated characters provides a well definable hiatus between it and *Suillus* as well as between the genus *Chalciporus* and the other genera of the Boletoideae and Xerocomoideae. These characters are: Neither yellow nor gray to pallid color of the entire hymenophore, yellow basal mycelium, absence of a veil, absence of clamp connections, absence of *Suillus*-like glandulae and *Leccinum*-like scales on the stipe which is smooth (non-reticulate), generally but not exclusively *Boletus*-type of hymenophoral trama, the gymnocarpic development and the characteristic assemblage of pigments. Furthermore, the frequently peppery taste and the erratic mycorrhizal association were factors which helped in deciding the position of this genus. On the other hand, I have observed in some species a degree of variability in the sequence of hymenophoral trama structures, which is never observed in *Suillus*.

*Chalciporus* differs from certain species of *Xerocomus* which may look similar, less in the configuration of the hymenophoral trama than in the combination of the other characters indicated above. Indeed, McNabb has described some species from New Zealand which he determined as *Xerocomus* because they have, according to him, *Phylloporus*-type of trama, but the color of the hymenophore would suggest *Chalciporus*. Particularly *X. aurantiacus* McNabb should be revised in view of the probability that it might be *Chalciporus* rather than *Xerocomus* and that the structure of the hymenophoral trama has been determined on not sufficiently young material, or that the structure of the trama is not as constant in *Chalciporus* as had

been assumed (it is likewise not constant in the related *Pulveroboletus*); the color of the hymenophore, the short spores, and the bright olive ammonia reaction (much like that of *C. rubinellus*) indicate affinity to *Chalciporus*.

Smith & Thiers have indicated their suspicion that two other species, recently with some hesitancy inserted in *Xerocomus*, might also be close to *C. piperatus*. These are *Boletinus castanellus* Peck and *Phylloporus squarrosoides* Snell & Dick. I have studied material of both species, but the anatomical data alone are insufficient to solve the problem of their position. I have formerly combined the species into a section of *Xerocomus (Pseudogyrodontes)* as a temporary solution, but it is quite possible that all these short-spored species are actually closer to *Chalciporus*, although the description of the color of the hymenophore (watery yellow and brown respectively) is not characteristic for that genus. Further studies are in order, preferably on material from the type locality.

*Pulveroboletus* is distinguishable from *Chalciporus* by the characters indicated in the key. *Tylopilus* may, in some species, have a similar spore print color, but the habit of the carpophores and the color of the hymenophore and the basal mycelium are so different that a confusion of the two can hardly be expected. The same is true for *Xanthoconium*. *Boletus* has likewise a different habit and different spore print color (before dehydration), and if the pores are red, the tubes are discolored (yellow) in the interior of the hymenophore.

*Rubinoboletus* (type species: *B. rubinus* W.G. Smith, undoubtedly a good species of *Chalciporus*) has been emended by Heinemann & Rammeloo (*Bull. Jard. Bot. Nat. Belg.* 53: 294-297. 1983) to accomodate all kinds of short-spored boletes, and transferred to the Gyrodontoideae. The resulting assemblage is highly artificial. Corner (1977, 1978) stated that "sporographic analysis shows that subglobose spores are to be expected in any alliance of elongated spores".

*State of knowledge:* Only seven species of *Chalciporus* are well enough known to the present author to be recognized as undoubtedly independent species belonging in *Chalciporus*. The genus should be revised and monographed and special attention should be given to the pigments, development of the carpophores (including colors), taste of the fresh carpophores, and chemical color reactions.

*Practical importance:* Unknown.

## SPECIES

*C. piperatus* (Bull. ex Fr.) Sing.; *C. rubinus* (W.G. Smith) Sing.; *C. rubinellus* (Peck) Sing.; *C. amarellus* (Quél.). Moser (*Boletus pierrhuguesii* Boud.); *C. pseudorubinus* (Thirring) Pilát & Dermek; *C. rubritubifer* (Kauffm.) Sing.\*; *C. trinitensis* (Heinemann) Sing., Araujo & Ivory\*\*\*; obviously also *C. corallinus* Pegler; *B.*

\*c.n. (*Boletus rubritubifer* Kauffm., *Bull. N. Y. State Mus.* 179: 88. 1915).

\*\*In Singer, Araujo & Ivory, *Nova Hedw. Beih.* 77: 86. 1983, the author citation should have been (Heinemann, *Bull. J. Bot. État* 24: 121. 1954) Sing., Araujo & Ivory, c.n. which is herewith corrected.

*pseudorubinellus* Smith & Thiers; *B. piperatoides* Smith & Thiers; *C. persicinus* Pegler; *B. rubriporus* Corner; probably also *Xerocomus aurantiacus* McNabb; *B. subflammeus* Berk., and *B. parvus* Peck.

## 215. PULVEROBOLETUS Murr.

*Mycologia* 1: 9. 1909; em. Sing. (1947).

*Type species:* *P. ravenelii* (Berk. & Curt.) Murr.

*Syn.:* *Aureoboletus* Pouzar, Česk. Myk. 11(1): 48. 1957 (Typus: *B. gentilis* Quél.).  
*Buchwaldoboletus* Pilát, Friesia 9: 217. 1969.

*Characters:* Hymenophore tubular, with narrow to wide pores, pores generally concolorous with the tube-interior, of various colors from pallid to bright reddish orange (but not dull red, carmine, wine-red, or pink), most frequently yellow, and often remarkably deep and bright in color which does not fade on drying (due to a pigment which is yellow and soluble in ammonia), hymenophoral surface either arcuate and tubes decurrent or soon becoming applanate or even strongly ventricose, and in this case more or less depressed around the stipe; hymenophoral trama either of the *Boletus*-type or (young) of the *Phylloporus*-type; clamp connections none in the hyphae of the carpophore and at the base of the basidia; spores more often elongate (cylindric-fusoid or oblong-fusoid) than short-cylindric or short-ellipsoid, sometimes pseudoamyloid; spore print brown with an olivaceous shade or olivaceous (before dehydration) "Isabella color" to "olive citrine" or "medal bronze", "light brownish olive" to "olive brown", "buffy olive" Ridgway, more rarely ferruginous-ochraceous without an olive tinge; cystidia rather large and conspicuous, ampullaceous or broadly ventricose-subclavate, somewhat incrusted or not; pileus often viscid when wet, even glutinous, or else covered by a yellow, green, yellow or brown pulverulence, at times only from a fugacious veil, at times becoming yellow-pulverulent on handling in dry weather (and then not necessarily viscid), centrally or somewhat eccentrically stipitate, rarely subsessile; epicutis in form of a cutis or ixocutis, more rarely a trichodermium or trichodermial palisade; veil present or absent, if present either strongly gelatinized and glutinous, or else pulverulent and then yellow, green, or with reddish-orange tinge; stipe equal or fusoid, more rarely ventricose and often attenuated into the base, surface smooth and glabrous or sometimes with a distinct reticulation of finely fibrillose-pulverulent or minutely pustulate, with an annular belt or belts or naked, often viscid or viscidulous, even glutinous, fleshy or cartilaginous and solid to hollow; basal mycelium yellow, or some other color, often white; taste not peppery; context bluing or not; ectomycorrhiza not formed in all species, lignicolous (on trunks or base of trees, on sawdust) or more often on the ground; ectomycorrhiza with *Quercus*, *Pinus*, *Shorea* demonstrable.

*Development of the carpophores:* Gymnocalyxous in *P. hemichrysus* according to Pantidou; metavelangiocarpous in other species (not known in detail) according to Watling.

*Area:* In the north-temperate and tropical zones, apparently absent or rare in the

boreal (arctic-subarctic), subalpine and alpine, and the south-temperate zones, but occurring on all continents except Antarctica.

**Limits:** The presence of pulverulent surfaces or even a pulverulent veil, or the presence of viscid stipe surface or even a glutinous veil separate *Pulveroboletus* well from *Boletus*, the spore color from the other genera of Boletoideae. The recently confirmed fact that some species of *Pulveroboletus* show a hymenophoral trama of the *Phylloporus*-type\* brings up the question about the limits of this genus against the Xerocomoideae. Since all species where chemical color tests have been made, show no trace of a positive (blue) ammonia reaction on the surface of the pileus, and since likewise no species with lamellar hymenophore are known whereas no species with pulverulent or glutinous veil are known in the Xerocomoideae, the delimitation does not meet with major difficulties. Species with either very bright and deep golden or orange hymenophore and viscidulous to glutinous stipe, and species with some detersile pulverulence on pileus and/or stipe and either reticulate stipe or arcuate-decurrent hymenophore belong to *Pulveroboletus*, not to *Xerocomus*.

The delimitation against *Boletus* was formerly obscured by the fact that *B. ornatipes* has been - apparently wrongly - identified with *P. retipes*, the latter being a not fully described, rare species. By retransferring the former to *Boletus* the limits become quite obvious.

Some, especially European authors have tended to restrict *Pulveroboletus* to its original species or section. As delimited here, however, and taking into account all species including the southern and tropical material, one cannot help but think that they form a natural group inasmuch as the characteristic habit (with arcuate hymenophore and decurrent tubes) of *P. hemichrysus* (with superficial pulverulence) and *P. lithocarpisequoiae* (glutinous veil) covers both the pulverulent and the glutinous groups. *P. ravenelii*, the type species, is really not basically different from the section *Auripori* except by the veil. Smith & Thiers have retransferred *P. lithocarpisequoiae* to *Suillus*, but I am afraid wrongly so, because it has no close relatives in *Suillus*, has no coniferous symbiont, and the habit and the glutinous veil are rather like many species of *Pulveroboletus* than *Suillus*. The cystidia are indeed more like the cystidia of *Suillus*, but incrusted cystidia do occur in *Pulveroboletus*. Unfortunately, no good spore print has been obtained from the type specimens, and if the spores (before dehydration) should actually lack an olive or ferruginous tinge, this species might be intermediate between *Suillus* and *Pulveroboletus*.

Since the recent discovery of an additional section of this genus, viz. *Duckeani*, which does not show the pulverulent or glutinous veil or the viscid stipe of most *Pulveroboleti*, we have to compare the genus also with *Boletus*. Only *Boletus* sect. *Subpruinosi* is similar in habit and pore size. In sect. *Duckeani*, the epicutis or hypodermium show a tendency to become gelatinized and the pileus is  $\pm$  viscid in wet

\*Some observations suggest that whenever a *Phylloporus*-type of hymenophoral trama was observed, this refers to young specimens which in the course of further development, through a progressing gelatinization of the lateral stratum, reach a stage which corresponds to the *Boletus*-type (in KOH mounts). Whether or not these observations can be generalized for this genus and also for *Chalciporus*, cannot be stated with certainty at present.

weather, the spores are pseudoamyloid, the stipe in *P. duckeanus* tends to become hollow, and there is apparently no ectomycorrhiza formed (see Singer, Araujo & Ivory 1983), all characteristics not typical for sect. *Subpruinosi*. Also the margin of the pileus is more acute and ± appendiculate in the *Pulveroboleti*.

The continuity between the type species with a fibrillose veil and the other sections is difficult to understand for those who are not familiar with representatives of all sections. At first glance, the pulverulent-arachnoid veil of *Pulveroboletus ravenelii* sets this species apart but the veil hyphae may be present and forming a pulverulence, more or less detersile, in other sections, and the gelatinization, present in the epicutis of *P. ravenelii* and related species, may become very strong in the ex-velar layer or even an indistinct velar layer leading to sections *Glutinovelati* and *Cartilaginei*. This gelatinized layer may be reduced to simply viscid pileus and stipe as in sect. *Auripori*, or else the gelatinization may be practically absent, as in sect. *Sulphurei*, or slow in forming and/or limited in extension as in sect. *Duckeani*. *Boletus xylophilus* is not a *Phaeogyroporus* (*Phlebopus*), nor a *Gyrodon*, but quite obviously a *Pulveroboletus*, sect. *Sulphurei*, where the detersile fibrillosity is seemingly or really lacking, and in this case a continuity between sect. *Sulphurei* and sect. *Duckeani* Sing. can be established. I have studied the respective types and additional material from Asia. The genus as a whole consists of species unrelated to species of *Xerocomus*, *Chalciporus*, and *Boletus* but the pulverulent-arachnoid surfaces, which may be replaced by glutinous surfaces, or the habit, the tendency of the stipe to become hollow and/or cartilaginous, the absence of blue reactions of the fresh surfaces with ammonia are characters common to the species of *Pulveroboletus* even where one of these characteristics should be missing in a given specimen. The transition from dry to glutinous species is neatly illustrated by the fact that Corner (1972: 134) describes *P. umbilicatus* as having a cover on the surface which is originally a dry, piloso-fasciculate tomentum then becoming mucilaginous. This statement is turned by Corner (p. 10) into a fact supporting his contention that *Pulveroboletus* is not a natural genus in my circumscription, while on the contrary, *P. umbilicatus* underscores the continuity of sections in this genus. As in other genera of mostly elongated-spored ('boletinoid') boletes, there is a tendency in *Pulveroboletus* towards short spores and, as in *Chalciporus*, there is a tendency of the hymenophoral trama to maintain a seemingly *Phylloporus* type of structure over longer periods, especially in species with reduced gelatinization or collected in dry periods.

It is understandable that it was European authors, unfamiliar with some sections of *Pulveroboletus*, who separated the split genera *Buchwaldoboletus* and *Aureoboletus* for the only two sections occurring in Europe. It goes by itself that Corner (1972) accepting an excessively wide circumscription of the genus *Boletus*, incorporated all *Pulveroboleti* in *Boletus*, but, following Smith & Thiers (1971) restricted the sub-genus *Pulveroboletus* to *P. ravenelii* which, according to him is, in contrast to other sections, 'angiocarpic'. But this is neither proved nor necessarily diagnostic on a generic level (*Xerocomus* contains paravelangiocarpic species), even if Corner's assumption should turn out to be correct.

Within the Boletaceae we find the genera *Xerocomus*, *Pulveroboletus*, *Chalciporus*, and *Boletus* rather similar in their pigments - a situation to be expected. On the

other hand, the separation of *Chalciporus* with variegatorubin as characteristic pigment (Besl, Bresinsky et al. 1975; Bresinsky 1974; Bresinsky & Rennschmid 1971; Singer 1975) from *Suillus* appears justified. The identical pigments of *Pulveroboletus hemichrysus* and *P. auriporus* show that species with dry as well as viscid surfaces can be chemotaxononomically indistinguishable in this genus, justifying both Singer (1975) who put them in two sections of *Pulveroboletus* and Smith & Thiers (1971) who put them in the same section (*Subtomentosi*) of *Boletus*, the former as *B. sphaerocephalus*. This is not in support of Corner (1972) who puts *Pulveroboleti* in three different subgenera of *Boletus* and refers to *Pulveroboletus* (on the basis of frequently erroneous statements and misdeterminations) as a 'dump for species, mostly tropical, which do not fit the alliance of temperate species of subgenus *Boletus*'. May it just be stated here that of the 24 species referred to *Pulveroboletus* by me 12 are tropical. Chemotaxononomically, the split genera *Aureoboletus* Pouzar (based on *P. gentilis*, closely allied to *P. auriporus*) and *Buchwaldoboletus* Pilát (based on *P. lignicola* - twice misspelled by Corner - closely related to *P. hemichrysus*) should be abandoned unless microgenera are admitted for every section of *Pulveroboletus*.

As for additonal comments on the status of *Pulveroboletus* see Singer, *Persoonia* 11: 269-302. 1981. See also under *Fistulinella* (p. 196).

*State of knowledge:* 24 species are here recognized as belonging to the various sections of this genus.

*Practical importance:* The mycorrhizal species of the genus are of possible importance in forestry inasmuch as they belong in part to the rare species associated with tropical trees of families such as the Dipterocarpaceae. Some species are edible. One (*P. viperinus*, i.e. apparently *P. xylophilus*) is considered poisonous in the Philippines.

## SPECIES

Sect. 1. *PULVEROBOLETUS*. (*Flavovelati* Sing. 1947). Veil pulverulent-arachnoid, sulphur yellow, greenish, or yellowish brown; hymenophoral surface soon flat or convex.

*Type species:* *P. ravenelii* (Berk. & Curt.) Murr.

*P. ravenelii* (Berk. & Curt.) Murr. (*Boletopsis icterina* Pat. & Baker); *P. frians* (Corner) Sing.\*; *Pulveroboletus annulatus* Heinemann and *P. croceus* Heinemann.

Sect. 2. *SULPHUREI* (Sing.) Sing. (1961). Veil strongly reduced or nil, but a brightly colored pulverulence or loose tomentum, both detersile or separable, usually visible on the surface of well dried material; hymenophoral surface not becoming convex and tubes adnexed to decurrent, often arcuate; stipe not extensively

\*c.n. (*Boletus frians* Corner, *Bolet. Malays.* p. 203. 1972).

reticulate or smooth, not viscid. Often on wood or sawdust and non-ectomycorrhizal.

Type species: *P. sulphureus* (Fr.) Sing.

*P. hemichrysus* (Berk. & Curt.) Sing. (*Boletus sulphureus* Fr. non Bull. ex Mérat; *Boletus sphaerocephalus* Barla); *P. lignicola* (Kallenbach) Pilát; *P. fragicolor* (Berk.) Sing.\*; *P. kivuensis* (Heinemann & Goossens) Sing. in Sing. & Grinling; *P. xylophilus* (Petch) Sing.\*\*; *P. leucomyccelinus* Sing. & Ivory.

Note: The two last-named species do not always show or tend to lose their pulverulent-velutinous covering on pileus and/or stipe. They thus show some sort of transition to sect. 4, especially where the hypodermium tends to gelatinize; they may be better placed in sect. 4. - Apparently here also a species with strongly reduced stipe: *P. acaulis* Pegler.

Sect. 3. *RETICULATI* Sing. (1947). Differs from sect. 2 in reticulate stipe.

Type species: *P. auriflammeus* (Berk. & Curt.) Sing.

*P. auriflammeus* (Berk. & Curt.) Sing.; *P. retipes* (Berk. & Curt.) Sing.

Sect. 4. *DUCKEANI* Sing. (1983). Veil and pulverulence none; covering layer of pileus in part becoming gelatinascent; context bluing; stipe solid or tending to become hollow; spores small, ellipsoid,  $\pm$  pseudoamyloid, not longer than about 8  $\mu\text{m}$ ; margin of pileus often involute or incurved at first; stipe not viscid. Tropical species, probably not or not obligatorily ectomycorrhizal, but not lignicolous.

Type species: *P. duckeanus* Sing. in Singer, Araujo & Ivory.

*P. duckeanus* Sing. in Sing., Araujo & Ivory, *P. rosaemariae* Sing. in Sing., Araujo & Ivory.

Sect. 5. *AURIPORI* (Sing.) Sing. (1947) (*Xerocomus* sect. *Auripori* Sing. 1942). Pores golden yellow or brightly olive-gold even in dried condition; veil either not abundant, or absent, pileus or stipe or both viscid; elements of the trama often filled with deep lemon yellow soluble (NH<sub>4</sub>OH) pigment; stipe covered by a gelatinous layer.

Type species: *P. auriporus* (Peck) Sing.

*P. subacidus* (Murr. ex) Sing. (*Ceriomyces*, Murr., nom. nud.); *P. auriporus* (Peck) Sing.; *P. cramesinus* (Secr.) Sing. (*Boletus sanguineus* var. *gentilis* Quél.); *P. thibetanus* (Pat.) Sing.\*\*\*; *P. innixus* (Frost) Sing.\*\*\*\*; *P. flavigiporus* (Earle) Sing.

Sect. 6. *GLUTINOVELATI* Sing. (1947). Veil strongly developed, forming an

\*c.n. (*Boletus fragicolor* Berk., *Hook Journ. Bot.* 4: 137. 1852).

\*\*c.n. (= *Boletus xylophilus* Petch, *Ann. R. Bot. Gard. Perad.* 7: 283. 1922; probably conspecific: *Phlebopus viperinus* Sing.).

\*\*\*c.n. (= *Boletus thibetanus* Pat., *Bull. Soc. Myc. Fr.* 11: 196. 1895).

\*\*\*\*c.n. (= *Boletus innixus* Frost, *Bull. Buffalo Soc. Nat. Sc.* 2: 103. 1874; = *B. auriporus* Peck sensu Coker & Beers = *P. caespitosus* (Peck) sensu Sing. (1947).

annulus whose outer layer is glutinous or becoming glutinous, eventually visible only as an appressed sheet; pileus also glutinous, or becoming so; surface corrugate or rugulose; spore print olive where known. Ectomycorrhiza if formed, not with conifers.

*Type species: P. corrugatus* (Pat. & Baker) Sing.

*P. umbilicatus* (Mass.) Sing. (*P. corrugatus* (Pat. & Baker) Sing.; *Boletopsis* Pat. & Baker); *P. lithocarpisequoiae* (Sing.) Sing. (Suillus, Sing. 1959).

Sect. 7. *CARTILAGINEI* Sing. (1947). Veil, if at all, not visible in mature specimens and not forming an annulus; pileus viscid or glutinous from the beginning or becoming so; stipe viscid or not, often cartilaginous and/or tending to be or become hollow; surface of pileus smooth or corrugated, or becoming scrobiculate on drying. Ectomycorrhiza, if formed, with Betulaceae, Dipterocarpaceae, Pinaceae. Spore print either olive or ferruginous.

*Type species: P. curtisii* (Berk.) Sing.

*P. curtisii* (Berk.) Sing.; *P. viridis* Heinemann; *P. shoreae* Sing. & Singh; *P. mazatencorum* Sing.; probably also *P. viscidulus* (Pat. & Baker) Sing. (cf. Singer, *Persoonia* 11: 284-285. 1981), *P. rufobadius* (Bres.) Sing. and *Ceriomyces atkinsonianus* Murr.

## 216. BOLETUS Dill. ex Fr.

*Syst. Mycol.* 1: 385. 1821, sensu str. Gilbert (1931) non al., nom. conserv.

*Type species: B. edulis* Bull. ex Fr.

*Syn.: Tubiporus* Paulet ex Karst., *Rev. Mycol.* 3: 16. 1881.

*Dictyopus* Quél., *Enchir.*, p. 159. 1886.

*Oedipus* Bat., *Bolets*, p. 13. 1909.

*Suillellus* Murr., *Mycologia* 1: 16. 1909.

*Ceriomyces* Batt. ex Murr., *Mycologia* 1: 144. 1909.

*Characters:* Cuticle (Pl. 77, 1-5) of the pileus rarely (in small tropical species) an epithelium; hymenophore consisting of small or large pores continuing into long tubes, depressed to almost free around the stipe in most specimens; hymenophoral trama truly bilateral-divergent of the *Boletus*-subtype; spore print olive or at least brown with an olive hue when quite fresh ("olive brown", "dark olive buff", "brownish olive", between "citrine drab" and "deep olive"); spores usually elongate (with variable shape, Pl. 52, 3, 5), but in some (especially tropical) species short; stipe usually thick and fleshy and solid, reticulate or finely flocculose-squamulose-subfurfuraceous, rarely smooth and glabrous, neither scabrous nor glandulose, evelate, without a distinct pseudosclerotium; context white or yellow, sometimes partly red, on injury often bluing, rarely reddening, mild or bitter; all hyphae without clamp connections; some species with amyloin-positive reaction especially in the base of the stipe of sections 2 and 4. Xerocomic and/or variegatic acid and derivatives present except in sect. 6 and in *B. ornatipes* (sect. 7). Obligatory ectotroph-formers mainly with Fagales (but rarely with *Alnus*) and Pinaceae, rarely with Tiliaceae, Polygonaceae and Leptospermataceae.

*Development of the carpophores:* Probably all gymnocarpous but not known in detail from recent investigations.

*Area:* Cosmopolitan, but most strongly represented in the warmer parts of the temperate zones, especially in North America and East Asia, only two\* species known from temperate South America (Chile) and two from the lowland neotropics.

*Limits:* As for the separation of *Boletus* from the preceding genera, see there. *Boletus* is well separated from *Tylopilus* in spite of what some European authors say about it. They know only one single species of *Tylopilus* and are not in a position to judge on the hiatus between the two groups. Aside from the color of the spore print which is sharply different in the two genera, there is also a difference in the darkening of the context in those species that are subject to autoxidation. This autoxidation provokes bluing in *Boletus*, and a variety of discolorations (reddish-gray, vinaceous, lilac, etc) in *Tylopilus*. *Boletus* is also well separated from *Xanthoconium* by the color and shape of the spores. In *Leccinum*, many species have the spore color of *Boletus* (or somewhat less olive). They are separated from *Boletus* by the roughness of their stipe. In some species with yellow pigment (sect. *Luteoscabra* of *Leccinum*) the scabrosities of *Leccinum* may be rather similar to the surface ornamentation of some *Boletus*-stipes. In this particular case, the author has taken to *Leccinum* the species with a definite cutis and viscid pileus as well as the species with an epithelium, while the species with trichodermium (Pl. 72, 1-4) and dry pileus remain in *Boletus*. Naturally, in some species of *Boletus*, the trichodermium forms a palisade (Pl. 72, 2-4) and the single members of the chains may become very short, and on the other hand in some specimens of *Leccinum rugosiceps*, the spherocysts of the epithelium may be somewhat elongated. In spite of such minor variations, the separation on this basis is rather sharp, and it leaves only a small number of species with epithelium in *Boletus*, and these are minute (Pl. 72, 9), tropical or not at all related to *Leccinum*. All species that may possibly be construed as intermediate between *Leccinum* and *Boletus*, are thus taken care of. This practical way of disposing of seemingly intermediate forms coincides with the strictly anatomical distinction: the asperulations on the surface of the stipe are considered characteristic for *Leccinum* only if their base consists of a well developed strand of parallel, thin hyphae - usually multiseptate - which end in a fragment of hymenium or a fascicle ending in basidia, dermatopseudoparaphyses and dermatocystidia. In the future our judgment on delimitation of *Boletus* vs. *Leccinum* may also be influenced by the fact that Kühner (1958) found the hyphal elements of the stipe of *Boletus* binucleate (or with up to 5 nuclei) whereas those of the typical species of *Leccinum* are ceno-cytic, i.e. contain a larger number of nuclei.

*State of knowledge:* 69 species have been admitted. A tentative key to the species has been published by Singer, *Sydowia* 30: 207-260. 1977.

*Practical importance:* Concerning their mycorrhizal properties, the *Boleti* have the

\*Horak (1977) has added two more species from the Valdivian region in Chile: *B. loyata* Horak (apparently sect. *Subpruinosi*) and *B. putidus* Horak (apparently sect. *Luridi*), both unknown to me (see *Bol. Soc. Arg. Bot.* 18: 97-109. 1977).

same chances as the neighboring genera to become interesting in forestry. At present, the main practical importance of the species of *Boletus* is their edibility. *B. edulis*, and related species of sect. *Boletus* belong to the most widely used and traded wild mushrooms in the world, at least as far as the temperate zones are concerned. They are exported from Eastern Europe and Italy, recently also from California, to various parts of the world, in dried as well as in pickled form. Fresh "cèpes", "hrby", and "Herrenpilze" are found in all European markets at the proper season but all efforts to grow them commercially have failed. Other species of this genus - as far as they have mild taste - are also highly estimated by mycophagists, but some species of the sect. *Calopodes* can spoil a whole meal by their bitterness. They should be carefully avoided. There have been controversies about the poisonous properties of *B. luridus*, *B. satanas*, and *B. miniatoolivaceus* (the three most poisonous species), and the response of various persons to the action of the poison as well as the violence of the poison itself varies a great deal. Even the three species named above are at times harmless. But if eaten by certain persons at certain localities in a certain quantity, even a small one, and especially if not cooked thoroughly\*, they may cause very serious poisonings. Phoebus published one case with *B. satanas*, where he himself had tested the species, and the symptoms are much the same as those experienced by the author when he had eaten *Boletus luridus*: Rapid action of the poison, excessive vomiting, psychological symptoms (depression), fast recovery. Epimuscarine has been found in *B. luridus* and *B. calopus* by Stadelmann et al. (*Helv. Chim. Acta* 59: 2434. 1976).

Heim (*Cahiers du Pacifique* no. 7, p. 9-23, 1965) indicates two species referable to *Boletus*, viz. *B. manicus* and *B. reayi* Heim as associated with the "folie des Kuma" or the "Wahgi River frenzies", in addition to four other boletes and the *Russula nondorbingi* Sing. previously (*Mycopath. Myc. Appl.* 9: 275-279. 1958) indicated as psychotropic by Singer. According to Heim, Dr. A. Hofmann has been able to ascertain the presence of three indolic substances in *B. manicus* but at present the active substances have not been isolated. Heim seems to be dubious about an immediate causative effect of these fungi since he speaks of fungi "prétendus responsables, selon les indigènes, du déclenchement de la folie" and avoids to call them psychotropic.

Two species have thus far been proved to have antibacterial properties: *B. radicans* and *B. satanas*.

## SPECIES

Sect. 1. *SUBPRUINOSI* Fr. (1874) em. Sing. (1947). Network on the stipe none or consisting of a narrow reticulate zone of decurrent pores immediately under the hymenophore, usually finely flocculose to furfuraceous, or fibrillose; context mild, changing or unchanging, more often bluing than not changing, never becoming

\*Even if thoroughly soaked, *B. satanas* can cause serious poisonings (cf. *Bull. Soc. Myc. Fr.* 100: 2. 1984).

pinkish gray or vinaceous, not containing poisonous substances in any known species; carpophores small (Pl. 72, 9) to medium sized, rarely large and with the habit of a *Xerocomus* rather than a *Boletus* (stipe not very thick and not ventricose or not much so); hymenophore adnate or slightly depressed around the stipe, more rarely deeply depressed, the pores medium sized (1 mm) to large in age, either distinctly open or daedaleoid-meandering and folded when young; surface of the pileus usually tomentose, or pruinose, or subtomentose, or velutinous, or granular.

Type species: *B. barlae* Fr.

*B. patouillardii* Sing.; *B. aureomycelinus* Pat. & Baker; *B. weberi* Sing. (this species and perhaps *B. parvus* Peck and "Pulveroboletus" *carminiporus* Heinemann belong in a well defined group, perhaps a separate section, characterized by red pores); *B. pulverulentus* Opat. (*B. mutabilis* Morgan); *B. fuligineotomentosus* Sing.; *B. caespitosus* Peck (sensu originali); *B. granulosiceps* Sing.; *B. subsolitarius* Sing., *B. rubellus* Krombh. (*B. versicolor* Rostk. non S.F. Gray; *B. sanguineus* With. non L. ex Lév. in Paulet, non Secr.; *B. rubripruinosus* Barla; *B. campestris* Smith & Thiers; *B. barlae* Fr.; *Xerocomus pruinatus* Quél.) with several subspecies (geographic races and mycoecotypes); *B. guadelupae* Sing. & Fiard; apparently also *B. fraternus* Peck; *B. rubeus* Frost.

Sect. 2. *LURIDI* Fr. (1838). Differs from the preceding section in smaller pores and generally more typical *Boletus*-habit in contrast to the *Xerocomus*-habit of most of the species of sect. *Subpruinosi*; pores more often discolored; surface of the stipe as in the preceding section but in some species finely to very strongly reticulate; pileus with a covering as indicated in the preceding section, or viscid; context often containing poisonous matter.

Type species: *B. luridus* Schaeff. ex Fr.

*B. impolitus* Fr.; *B. fragrans* Vitt.\*; *B. rubricitrinus* (Murr.) Murr.; *B. luridellus* (Murr.) Murr.; *B. fairchildianus* (Sing.) Sing.; *B. reayi* Heim; *B. flavissimus* (Murr.) Murr.; *B. miniatooolivaceus* Frost; *B. underwoodii* Peck; *B. subluridus* (Murr.) Murr.; *B. junquilleus* (Quél.) Boud.; *B. caucasicus* (Sing.) Sing.\*\*; *B. chilensis* Sing.; *B. queletii* Schulzer; *B. dupainii* Boud.; *B. loyo* Phil. ex Spec.; *B. austrinus* Sing.; *B. tomentipes* Earle; *B. michoacanus* Sing.; *B. rhodopurpureus* Smotlacha; *B. hypocarycinus* Sing.; *B. subvelutinus* Peck; *B. vermiculosus* Peck; *B. fuscopunctatus* Hongo & Nagasawa; *B. erythropus* (Fr. ex Fr.) Pers.; *B. morrisii* Peck; *B. eastwoodiae* (Murr.) Sacc. & Trotter; *B. rhodoxanthus* (Krombh.) Kallenbach; *B. satanas* Lenz; *B. luridus* Schaeff. ex Fr.; *B. lupinus* Fr. (sensu Romagnesi); *B. splendidus* Martin (*B. satanoides* Smotlacha) with ssp. *splendidus* and ssp. *moseri* Sing. & Kuthan; *B. torosus* Fr. in Fr. & Hök; *B. frostii* Russel; *B. floridanus* (Sing.) Sing.; apparently also *B. dichrous* Ellis; *B. sullivantii* Berk. & Curt. apud Mont.; *B. magnisporus* Frost; *B. firmus* Frost; *B. fagicola* Smith & Thiers; also the following Asiatic species: *B. rufoaureus* Mass. (*B. flammeus* Heim); *B. manicus* Heim; *B.*

\*In the sense of some French mycologists, this is a *Xerocomus*, probably the atypical fall-winter form of *X. chrysenteron*, and perhaps near *B. mendocinensis* Thiers.

\*\*[ex Alessio]. The validity of the basionym is doubtful according to Art. 35.2, H 10.3.

*quercinus* Hongo; *B. craspedius* Mass.; *B. magnificus* Chiu.

**Note:** The discolorous (reddish orange, carmine red etc.) pores on which the section was originally based and which provides a good macroscopic field character, cannot be used for the distinction of sections in *Boletus* since it does not only occur likewise in sect. *Subpulverulenti* (see above) but also in *Xerocomus* and *Pulveroboletus* as well as in *Boletellus* (see *X. nothofagi* McNabb, *Pulveroboletus auriflammeus* (Berk. & Curt.) Sing. and *Boletellus pictiformis* (Murr.) Sing.). In each case a series or stirps may be based on discolorous pores, but, basically, it is a specific character in a natural arrangement.

Sect. 3. *APPENDICULATI* Konr. & Maubl. (1924-37). Context more or less yellow, bluing, more rarely unchanging, mild; hymenophore yellow; stipe distinctly reticulate; pores not or scarcely discolorous, never red; context not containing poisonous substances; pileus dry or subviscid.

*Type species:* *B. appendiculatus* Schaeff. ex Fr.

*B. auripes* Peck; *B. appendiculatus* Schaeff. ex Fr.; *B. fechtneri* Velen. [*B. pallescens* (Konrad) Sing.; *Boletus appendiculatus* ssp. *pallescens* Konrad]; *B. speciosus* Frost; *B. regius* Krombh.; probably also *B. fibrillosus* Thiers.

Sect. 4. *CALOPODES* Fr. (1838), sensu str. Sing. (*Pachypodes* Konr. & Maubl. 1924-37). Context white to yellowish, bitter; tube wall bluing when fresh.

*Type species:* *B. calopus* Fr.

*B. frustosus* Snell & Dick; *B. radicans* Pers. ex Fr. sensu Kallenbach (*B. albidus* Rocqu.); *B. inedulis* (Murr.) Murr.; *B. calopus* Fr.; *B. peckii* Frost apud Peck; *B. pallidus* Frost.\*

Sect. 5. *BOLETUS* (*Edules* Fr. 1938). Context white and unchanging (or at least not bluing except in very rare cases in which a slight bluing is observed near the tubes), mild; stipe quite smooth to distinctly reticulate; spores elongate; epicutis (Pl. 72, 1-2) not an epithelium, tubes white, later yellowish, then greenish in some species, or pores occasionally slightly brownish; cystidia not strongly colored.

*Type species:* *B. edulis* Bull. ex Fr.

*B. atkinsonii* Peck; *B. nobilis* Peck; *B. aereus* Bull. ex Fr.; *B. violaceofuscus* Chiu; *B. quercicola* (Vassilkov) Sing.; *B. pinophilus* Pilát & Dermek; *B. clavipes* (Peck) Pilát & Dermek; *B. multipunctus* Peck; *B. separans* Peck; *B. aestivalis* (Paulet ex) Fr.; *B. edulis* Bull. ex Fr.; obviously also *B. betulincola* (Vassilkov) Pilát; *B. carpinaeus* Velen.; *B. variipes* Peck; *B. chippewaensis* Smith & Thiers; *B. subaereus* Pilát (perhaps only a form of *B. aereus*), and *B. mamorensis* Redeuil.

Sect. 6. *GRISEI* (Sing.) Sing. (1946). Tubes white, later grayish; cystidia strongly colored (melleous or fuscous brown inside); variegatic and xerocomic acid and known derivatives absent and thus differing from sections 1-5.

*Type species:* *B. griseus* Frost apud Peck.

\*The latter species is somewhat intermediate between sect. 3 and 4 as these are defined at present.

*B. griseus* (Frost apud Peck), ssp. *griseus* and spp. *pini-caribaeae* Sing.; *B. fumosiceps* (Murr.) Sing.

Sect. 7. *ORNATIPEDES* Sing.\* Differs from the preceding section only in the presence of a bright yellow pigment in all parts of the carpophore; reticulation of the stipe (as in the type species of sect. 6) strongly raised (more so than in sect. 3); context staining deeper yellow, not bluing, ± bitter. KOH on pileus yellow.

Type species: *B. ornatipes* Peck.

*P. ornatipes* Peck.

Note: Chemotaxonomically and in cystidial characters sect. 6 and 7 approach *Tylopilus* but the olive hue in the fresh spore print is that of *Boletus*.

## 217. BOLETELLUS Murr.

*Mycologia* 1: 10. 1909; em.

Type species: *B. ananas* (Curt.) Murr.

Syn.: *Boletogaster* Lohwag, *Beih. Botan. Centralbl.* 42(2): 274. 1931.

*Frostiella* Murr., *Mim. Contrib. Herb. Univ. Fla. Agr. Exp. Sta.*, Jan. 5, p. 6. 1942 (nom. nud.).  
*Heimiella* Boedijn, *Sydowia* 5: 217. 1951 (publ. 1952).

**Characters:** Pileus scaly, or naked, dry or viscid; hymenophore with yellow colors, sometimes with red pores; spore print from deep olivaceous to olive brown; spores well colored under the microscope, either smooth and then over 20 µm long or with imbedded short spines (punctate from above), or most frequently winged or ridged from "pole" to "pole" (Pl. 78, 7, 9-10), also reticulate in some species, always elongate, except in some species with reticulate ornamentation; ornamentation generally visible under a good oil immersion lens; hyphae with or more frequently without clamp connections; hymenophoral trama of the *Boletus*-type. On the soil, rarely on the base of trees or on very decayed wood.

**Development of the carpophores:** Probably often either primarily or secondarily angiocarpous; in several species (incl. *B. zelleri*) gymnocarpous.

**Area:** North America and pantropical; in Europe only one species, in Japan several.

**Limits:** The olivaceous spore print and the yellow hymenophore are characteristic enough to avoid difficulties within the boletes with ornamented spores. All species which have these characters belong either to *Boletellus* or to *Phylloboletellus*. However, there are three species (sect. *Mirabiles*) which although they have very large spores (over 18 µm reaching over 30 µm) and do not differ from other sections of the genus except by completely smooth and homogeneous spore wall, have, because of this latter character, not always been recognized as Boletelli. However, when transferred to *Boletus*, they have no visible affinity among the species of that genus and

\*sect. nov. A sectione *Griseorum* differt hymenophoro, stipite, carne laete flavis. Typus: *B. ornatipes* Peck.

are kept together and separated from the rest of the species in an infrageneric taxon of their own. The surface of these species is rough-fibrillose-squarrose or velutinous-squamulose on mature pilei, and the spore size has no equivalent in either *Xerocomus* or *Boletus*. The hymenophoral trama is of the *Boletus*-type, and therefore *Xerocomus* is also anatomically different.

In *Boletus* sensu str. Pegler & Young (1971, 1981) show only smooth-spored replicas. The spores are 'remarkably uniform in appearance' which is remarkable inasmuch as *Boletus* shares with *Boletellus zelleri* and *B. intermedius* the structure of the hymenophoral trama. In macroscopical characters *Boletellus* comes close only to section *Subpruinosi* of *Boletus*.

Since Pegler & Young's (1981) classification is derived basically from spore morphology it is not surprising that a different ornamentation such as we have in *Boletellus* sect. *Retispori* (*Heimiella*) as compared with that of the remaining species, or the different ornamentation of *Afroboletus* as compared with that of sect. *Strobilomyces* has led the authors to recognize the genera *Heimiella* and *Afroboletus*, and to transfer *B. betula* to *Austroboletus*, which is classified in another family in Pegler & Young's scheme. Fortunately this transfer is modified by the remark 'The olivaceous tint of the spores raises the possibility that this species may have a closer relationship with Boletaceae than with Strobilomycetaceae.'

How different spore ornamentation types can be in *Austroboletus* becomes clear when available photomicrographs are compared (Moser, 1978: pl. 45; Arpin & Kühner, 1977: 29, figs. 131-139; Watling & Largent, 1977: figs. 20, 22, 23, 25-28, 31, 36). Why, then, should *Heimiella* and *Afroboletus* be separated from *Boletellus* respectively *Strobilomyces*? We see that here we have *Boletellus* spores ranging from smooth (if we admit sect. *Mirabilis*) to faintly longitudinally veined, winged or reticulate. In *B. betula* we find the 'coalescence of the alveoli often producing the individualization of a "pillar"' (Perreau & Heim) while the light microscope shows what appears like pillars forming an ornamentation type XI (Singer, 1975). A similar ornamentation type is known in *B. alveolatus* (Heim & Perreau) Sing. Judging by the spore color and the yellow color of context and other parts of the carpophore, we may anticipate that all Boletelli are chemically similar to the species where pigment studies have already been made (cf. Bresinsky and collaborators).

Corner and some others seem to think that *Boletellus* if smooth-spored would be close to *Xerocomus*. This is correct as far as habitus is concerned, but incorrect with regard to the structure of the hymenophoral trama which is of the *Phylloporus*-type in *Xerocomus* and of the *Boletus*-type in *Boletellus* (see pl. 25), verified in nearly all species referred to *Boletellus* by me. The misinterpretation of the trama structure by Corner may have to do with his method of using alcohol-formalin or, as with Heim, with studying a non-suitable stage of development of the carpophore. Thus smooth-spored species would not be like *Xerocomus* inasmuch as they often have small pores depressed around the apex of the stipe. They would rather be like *Boletus*, and in habit much like sect. *Subpruinosi* where, however, the species with stipes showing coarse elevated ridges forming alveoli as found in sections *Dictyopodes* and *Allospori* would be out of place, as would be clamp bearing species as *B. fibuliger*.

I said (Singer 1975: 744, 750) that 'I am certain that modern pigment analysis will confirm, however, that *Strobilomyces* and *Boletellus* are chemotaxononomically different' and that 'spore sections under E.M. and pigment analyses will eventually decide whether a subfamily or a family Strobilomycetoideae or Strobilomycetaceae is preferable.' The first of these statements has been clearly decided (Bresinsky & Besl 1979) in the sense expected by me; the second has been decided (see p. 801). Chemotaxonomy would suggest that *Boletellus* is amply different from the other "strobilomycetaceous" genera except *Phylloboletellus* which seems to have a similar relationship to *Boletellus* as *Phylloporus* has to *Xerocomus*. The former pair has an olivaceous spore print, yellow colors in hymenophore and context, occurrence of clamp connections (one species with numerous clamps - *B. fribuliger*, few and often 'false' clamps in *Phylloboletellus*) as well as either gigantic or ornamented spores in common, aside from a predominantly tropical-subtropical distribution and a bilateral hymenophoral trama of the *Boletus*-type. This is in contrast to *Austroboletus* and *Porphyrellus*, as well as to *Strobilomyces* and *Xanthoconium*, *Tylopilus* and *Fistulinella*, one section or two of *Boletus*, and several species of *Leccinum*. In all these except the last two, the spore print is never olivaceous (fresh, not dehydrated), and all the data now available seem to indicate that there is a certain continuity here which cannot be expressed by separating the genera by spore ornamentation alone.

*State of knowledge:* 33 species are now known to belong to this genus, all of which I have studied personally.

*Practical importance:* Some species are edible but neither in quality nor in economical importance are they comparable to the edible species in *Boletus*. Some species appear to be at best only facultatively ectomycorrhizal while others are definitely obligatorily ectomycorrhizal and therefore of some potential importance in forestry. Some belong in the group of fungi used in New Guinea and considered hallucinogenic or psychotropic (see under *Boletus*). Lee & al. (*Lloydia* 38: 451. 1975) found the alkaloids hordenine, tyramine and N-methyltyramine in what they identified as *B. zelleri*.

## SPECIES

Sect. 1. *BOLETELLUS*. Pileus not or scarcely viscid, mostly with reddish pink or vinaceous-purple pigments, the margin often appendiculate by a conspicuous veil-like membranous structure which rings the stipe in young specimens, often with a strongly soft-squamose surface much like that of *Strobilomyces floccopus* or *Gastroboletus fascifer*; stipe not viscid and not waxy lacunose-alveolate; spores voluminous and all or many of them reaching a length of over 16  $\mu\text{m}$  and/or a breadth over 9  $\mu\text{m}$ , longitudinally winged, costate, or striate, the wings vertically finely striate or not (if wings smooth - pileus with strongly projecting margin); clamp connections none.

*Type species:* *B. ananas* (Curt.) Murr.

*B. ananas* (Curt.) Murr. (with var. *ananas*, var. *crassotunicatus* Sing. and var. *minor* Sing. (*Strobilomyces pallescens* Cooke & Mass.; *S. ligulatus* Cooke; ?*Boletus* gua-

*delupensis* Pat.\*); *B. verrucarius* (Berk.) Sing.; *B. squamatus* (Berk.) Sing.; *B. paradoxus* (Mass.) Gilb.; *B. emodensis* (Berk.) Sing.; *B. annamiticus* (Pat.) Gilb.; *B. floriformis* Imazeki; *B. porphyrius* (Pat. & Baker) Gilbert (the last five probably conspecific, with *emodensis* the oldest epithet); *B. rufescens* (Cooke & Mass.) Sing.; *B. ananaecepis* (Berk.) Sing.; *B. immutabilis* (Bouriquet) Perreau; evidently also *B. dissiliens* (Corner) Pegler & Young; *B. ananas* Curt. sensu Corner.

Sect. 2. *MIRABILES* Sing. (1945). Differing from sect. 1 in smooth spores, these elongated and reaching over 20 µm in length; Margin of pileus mostly ± projecting and/or with ± thickened cystidial wall; reddish pigments less prominent. Not bluing but often staining yellow. In temperate and tropical-montane forests, often lignicolous, associated with Pinaceae and Fagaceae.

Type species: *Ceriomyces mirabilis* Murr.

*B. mirabilis* (Murr.) Sing.; *B. projectellus* (Murr.) Sing.; obviously also *Boletus ascendens* Corner.

Sect. 3. *RETISPORI* Sing. (1945). Differs from the preceding sections in reticulate spores (ornamentation type I) most, often all, spores less than twice as long as broad.\*\*

Type species: *B. retisporus* (Pat. & Baker) Sing.

*B. retisporus* (Pat. & Baker) Sing.; *B. ivoryi* Sing. in Sing., Araujo & Ivory; obviously also *Heimiella anguiformis* Heim, *H. subretispora* Corner, *H. rubropuncta* Hongo, *H. kinabaluensis* Corner, *H. japonica* Hongo, and (pileus glutinous) *Boletus mandarinus* Ces.

Sect. 4. *CHRYSENTEROIDEI* Sing. (1945). Spores longitudinally winged, ridged, or striate, sometimes very low-ornamented, if winged, the wings not perpendicularly striate and the sterile, projecting margin of the pileus not developed or absent; pileus and stipe not glutinous or viscid; stipe not waxy lacunose-alveolate. Clamp connections present or absent.

Type species: *B. chrysenteroides* (Snell) Snell.

*B. lepidosporus* Gilbert ex Heinemann; *B. pictiformis* (Murr.) Murr.; *B. fallax* (Sing.) Sing. (non *Boletus fallax* Corner, also of this section); *B. lindneri* Sing.; *B. pustulatus* (Beeli) Gilbert; *B. chrysenteroides* (Snell) Snell; *B. hiratsukae* Nagasawa; *B. pseudochrysenteroides* Smith & Thiers; *B. zelleri* (Murr.) Sing., Snell & Dick; *B. intermedius* Smith & Thiers; *B. umbrinellus* (Pat. & Baker) Sing. in Sing., Araujo & Ivory; *B. obscurecoccineus* (Höhn.) Sing.; *B. cubensis* (Berk. Curt.) Sing. (?*B. lignatilis* Berk. & Curt.); apparently also *B. cardinalicus* Heim & Perreau and *B. episcopalis* Heim & Perreau as well as *B. rubroviolaceus* Heinemann & Goossens and *B. longipes* Heinemann (non *Boletus longipes* Mass.). Also here: *B. fibuliger* Sing. in Sing., Araujo & Ivory (with clamp connections).

\*see Singer, Araujo & Ivory (1983, p. 156-157).

\*\*The shortness of the spores alone is not a decisive character; neither are the ridges reaching the top of the spore (cf. *B. badiovenosus* Horak, *Kew Bull.* 31: 650-651, 1976).

Sect. 5. *Ixocephali* Sing. (1945). Spores longitudinally winged or costate as in sect. 1, 4 but sterile surfaces of the carpophore viscid to glutinous (strongly gelatinized), the margin often widely projecting and appressed to the young stipe, later appendiculate, or not projecting; stipe not waxy-lacunose-alveolate; apparently angiocarpous. Tropical.

*Type species:* *B. singaporenensis* (Pat. & Baker) Sing.

*B. longicollis* (Ces.) Pegler & Young (Boletus, Cesati; Boletopsis singaporenensis Pat. & Baker; Boletellus, Sing.; Boletus altissimus Mass. according to Corner and Pegler & Young); *B. jalapensis* (Murr.) Gilbert (Ceriomyces, Murr.; Boletogaster, Lohwag).

Sect. 6. *Dictyopodes* Sing. (1945). Pileus not viscid or scarcely subviscid, otherwise like sect. 5 but stipe with a prominent waxy-lacunose-alveolate network or anastomosing ridges; hyphae without clamp connections. Temperate species.

*Type species:* *B. russelii* (Frost) Gilbert.

*B. russelii* (Frost) Gilbert.

Sect. 7. *Allospori* Sing. (1945). Spores with immersed short cylindric plugs and/or broad irregular bands, with holes between them (ornamentation type XI) or similarly verrucose (light microscope) whereby they appear similar (in SEM) to *Austroboletus* spores but carpophore and spore pigments different; hyphae amyloid according to Heinemann; clamp connections absent; stipe lacunose-alveolate.

*Type species:* *B. betula* (Schwein.) Gilbert.

*B. betula* (Schwein.) Gilbert; obviously also *B. alveolatus* (Heim & Perreau) Sing.

Sect. 8. (unamed). Differing from sect. 7 in the absence of a distinct alveolate reticulation on the stipe. Further characteristics of the section seem to be: Small size of the carpophores, absence of an ixotrichodermium on the pileus which is dry and coarsely verrucose, the relatively wide pores.

Here: *B. purpurascens* Heinemann; *B. shichianus* (Teng & Ling) Teng, and *Austroboletus latitubulosus* Horak.

## 218. *Phylloboletellus* Sing.

In Sing. & Digilio, *Lilloa* 25: 438. 1951 (publ. 1952).

*Type species:* *Phylloboletellus chloephorus* Sing. in Sing. & Digilio.

*Characters:* Pileus with acute margin which is incurved, fleshy; hymenophore lamellate, lamellae broad, generally somewhat intervenose, decurrent, somewhat waxy; veil none; context turning blue where wounded; habit somewhat like that of *Gomphidius* or *Phylloporus*; spores medium to large, elongated, ornamented (with longitudinal wings in the only species known), deep olive in print; large cystidia present; hyphae without true clamp connections or with many clamp connections together with many simple septa. On the ground in subtropical and subtropical-montane forest.

*Development of the carpophores:* Unknown.

*Area:* Subtropical-montane forest zone in Southern South America and Mexico.

*Limits:* This differs from the Paxillaceae and Gomphidiaceae as well as from the Boletaceae (*Phylloporus*) in the ornamentation of the spores. This ornamentation is exactly as in some boletes of the preceding genus (sect. 3-6) from which this genus differs in lamellate hymenophore. The deep olive spore print is also in agreement with *Boletellus*. The (somewhat erratic) clamp connections remind one of *Boletellus fibuliger*. The relation between *Phyllobolotellus* and *Boletellus* is comparable to that between *Phylloporus* and *Xerocomus* in the Xerocomoideae.

*State of knowledge:* A single species is known since 1952. This species is completely known.

*Practical importance:* Unknown; the type species grows in a forest type which is considered anectotrophic and no ectomycorrhiza forming trees have been observed in the vicinity of the three localities where it has been observed.

## SPECIES

*P. chloephorus* Sing. in Sing. & Digilio.

### 219. LECCINUM S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 646. 1821; em. Snell (1942).

*Type species:* *L. aurantiacum* (Bull. ex St-Amans) S.F. Gray.\*

*Syn.:* *Krombholzia* Karst., *Rev. Mycol.* 3: 17. 1881, non Rupr. ex Galeotti (1844) nec *Krombholzia* Benth. (1881).

*Trachypus* Bat., *Bolets*, p. 12. 1908, non Reinw. & Hornsch. (1826).

*Krombholziella* R. Maire, *Publ. Inst. Bot. Barcelona* 3(4): 41. 1935.

*Characters:* Pileus with a cuticle consisting of an epithelium (Pl. 77, 7) or with only a few spherocysts, or with some chains of broad and short hyphae mixed in along with filamentous hyphae of a trichodermium, or the cuticle made up by a cutis consisting of filamentous, horizontally arranged hyphae at least in the upper stratum, viscid or dry, glabrous, granulose, or tomentose, often rimose or rimulose-areolate, the margin often sterile and membranous, projecting as a continuation of the cuticle and the marginal trama (and sometimes interpreted as an appendiculate veil); hymenophore yellow or yellowish, or whitish to sordid, convex beneath, the tubes very long in comparison with the diameter of the context and the radius of the pileus, but drastically shortened around the stipe and almost free, or free when adult, pores

\*The type species was changed by Snell (1942) without indication of a proper reason why Murrill's earlier choice should be changed, and Sutara (1982) believed that the type should be *L. edule* (Bull. ex Fr.) S.F. Gray. S. Rauschert (*Zeitschr. f. Mykol.* 49: 243-247. 1983) has, for reasons with which I fully agree, rejected Sutara's conclusions.

very fine to small (less than 1 mm in diameter) and the walls between the tubes also very thin (consequently also the trama a very thin layer); pores never discolored but sometimes stained because of discoloration from autoxidation after injury; hymenophoral trama truly bilateral-divergent of the *Boletus*-subtype; spore print olivaceous umber to umber or even cinnamon-brown in non-dehydrated print "olive brown (Ridgway) to "Clove" (Maerz & Paul) or (in one section) sordid vinaceous-wood-brown to "ferruginous" Ridgway, or pinkish argillaceous or flesh brown ("vassar tan" to "marron glace", after dehydration "tanbark" or "terrapin"); spores (Pl. 52,6) under the light microscope fusoid cylindric or fusoid-oblong, strongly elongated and rather large (to very large in some species reaching more than 20  $\mu\text{m}$  on length) smooth; cystidia (Pl. 77,6) fusoid-ventricose or ampullaceous in most cases, not of the oleocystidium-type, usually hyaline, small to medium sized; stipe usually relatively thin at the apex when mature and here easily breaking, with harder and more fibrous consistency than the pileus, most frequently obclavate-broadened below, more rarely subequal or slightly attenuated towards the apex, not bulbous-ventricose in the manner of *Boletus*, neither with glandular dots nor with soft pustules, but with rough asperulation furfuraceous-scaly on usually (at least in mature specimens) much paler or white ground, these ornamentations at maturity pigmented, with a basal hyphous portion consisting of a bundle of parallel filamentous, often multiseptate hyphae and ending in a hymenium-fragment or fascicle of differentiated elements (Pl. 40), basidia, dermatopseudoparaphyses\* and dermatocystidia, these asperulations at times connected with each other by a network, but stipe never reticulate without asperulations; never sticky or glutinous, rarely with, mostly without a veil (but the frequently projecting sterile margin of the pileus at times seemingly velar), without a pseudosclerotium; mycelium directly connected with ectomycorrhizal tree roots, associated with Fagales and Salicales, rarely *Pinus* and Ericaceae, ?*Cistus*; context yellow or white, changing or unchanging by autoxidation, often discolored in the base of the stipe (yellow, blue); all hyphae without clamp connections (but the elements of the scabrosities of the stipe with occasional (false?) clamps in some species (but even then base of basidia not clamped).

*Development of the carpophores:* At least two species are pilangiocarpous and stipitocarpous (Watling 1985).

*Area:* From the arctic regions to the subtropics; according to Corner 1972 and Heinemann (1964) also in the Asiatic and African tropics, but most species and individuals in the north-temperate zone; absent in South America except in plantations.

*Limits:* *Leccinum* is easily recognized even in the field by its macroscopical characters. Smith & Thiers (1971) have taken some species of section 1 to *Boletus* and the species of section 3 and 4 to *Tylopilus*. As for the former, it appears that they wish to exclude *L. rubropunctum* and *L. subglabripes* from the Leccina but, because of some error of typing or printing, their data on *B. longicurvipes* and *B. rubropunctum* are mixed up and unintelligible (p. 313-315) so that one has to go back to a note by the same authors (*Mycologia* 60: 949-945. 1967) in order to find that their principal ob-

\*These have been renamed "caulobasidioles" by Smith & Thiers (1971) but since they are permanently sterile, they are not homologous with basidioles.

jection to these species being Leccina is the notion that their stipe-ornamentation is not darkening (enough). Since this is a matter of degree as is clear from my own as well as Smith & Thiers' descriptions, it must be taken into consideration that these two species are obviously closely related to the yellow-pored species left in *Leccinum*. They are not closely related to any existing section of *Boletus* so that they were separated by Smith & Thiers in a special section *Pseudoleccinum*. Under the circumstances, I cannot but adhere to my original delimitation of *Boletus* and *Leccinum* (see also under *Boletus*). As for *Leccinum* sect. *Roseoscabra*, it is an obvious overemphasis on spore print color in a genus with admittedly very wide ranges of spore color, to insist on the only differentiating character other than the spore color, i.e. the allegedly not darkening scabrosities of the stipe. A glance at Snell & Dick's magnificent plate (71) shows that the scabrosities are indeed darker than the fundamental color even if they tend to red rather than black as, indeed they also do in *L. rubropunctum* and, for that matter, in *L. subpulchripes* Smith & Thiers. In addition, *L. chromapes* has the habit, the differentiated stipe-base-color, the large spores, the cystidia, and the anatomy of the scabrosities of *Leccinum* - in short all essential characters of *Leccinum* whereas in *Tylopilus* it has so little affinity that Smith & Thiers erected a special subgenus for it: *Roseoscabra* (Sing.) Smith & Thiers.

As far as pigments are concerned - not only those of the spore print but those of the carpophores and the mycelium in culture - *Leccinum* obviously occupies a transitional position between the basically olive spored and the basically pink spored genera. While sect. 1 is still closer to *Boletus*, sect. 4 is near *Tylopilus* where it was placed until Pomerleau (1959) and I found that it is nearer *Leccinum*. The structure of the scabrosities of the stipe, the often extremely long spores (up to 23.5 µm), the projecting sterile margin, the type of hymenial cystidia, and the whole appearance (see Snell & Dick, *The Boleti*, pl. 59) have caused me to accept Pomerleau's suggestion (1973).

Fortunately the scabrosities of the stipe, the anatomy of these scabrosities, and the general habit of *Leccinum* have served as a unifying character, accompanied by many secondary characters, to keep this natural unit, restricted to the northern hemisphere and extremely rich in forms in the north-temperate zone, intact. Even the chemotaxonomy - unfortunately less productive in pertinent data on *Leccinum* than on the preceding genera - gives some indication on the continuity of the genus by demonstrating gyroporin and atrotomentinic acid in some *Leccinum*-species including *L. eximium*.

*State of knowledge:* The genus is apparently richer in species than was originally thought. It has been revised both in North America and Europe in recent years (Smith & Thiers & Watling 1966; 1967; Blum 1968, Pilát & Dermek 1974, Smith & Thiers 1971, Thiers 1975 and others). Mycologists who have watched the number of species grow in regions where they had been accustomed to distinguish only a few, will undoubtedly feel that the species concept of the authors involved is smaller and describes, in certain cases, populations of a fleeting series of forms rather than species as otherwise recognized in Boletaceae; yet, be this as it may, it will be neces-

sary for anyone attempting to determine Leccina, to consult the papers quoted above. They represent an enormous and commendable effort to catalogue and distinguish whatever has been found in these regions; they have brought forward some new and valuable characters, and they have corrected a few errors, for example my erroneous identification of an American species (*L. snelli* Smith, Thiers & Watling) as *L. oxydabile* (Sing.) Sing.

While further revisions will undoubtedly introduce new aspects and check on the value of the older characters and add, it may be expected, additional taxa from thus far neglected areas, I refrain from adding species I have not studied myself and indicate in the following survey only a few representatives of each group, altogether 24.

**Practical importance:** All known species seem to be edible, some are used for food and sold in the markets, prepared fresh, dried, salted or pickled. The Leccina may also become important for forestry since they are rather specialized ectomycorrhizal fungi.

## SPECIES

Sect. 1. *LUTEOSCABRA* Sing. (1947). Hymenophore and usually also stipe and at least a part of the context yellow or yellowish; spore print "olive brown" (Ridgway) or some similar color with a distinct olive tinge.

*Type species:* *L. nigrescens* (Richon & Roze) Sing.

*L. subglabripes* (Peck) Sing. (*Boletus*, Peck); *L. rubropunctum* (Peck) Sing.; *L. rugosiceps* (Peck) Sing.; *L. nigrescens* (Richon & Roze) Sing. [*L. crocipodium* (Letellier) Watling sensu Watling - but Letellier's binomial not validly published and doubtful]; *L. extremiorientale* (L. Vassilieva) Sing.; *L. corsicum* (Roll.) Sing. (?*L. hispanicum* Moreno); perhaps here *B. squarrosipes* Corner.

*Note:* Bresinsky & Besl's (*Zeitschr. f. Mykol.* 45: 247-264. 1979) chemotaxonomical data suggest that *L. subglabripes* and *L. rubropunctum* (with xerocomic and variegatic acid and without gyroporin) are different (and may require a special section) from those species chemotaxonically (without xerocomic and variegatic acid) like *L. rugosiceps*. With the few and still scattered data at hand, this is at present taxonomically impossible to carry out. It has nevertheless been attempted by Smith & Thiers (1971) who separated *L. subglabripes* and *L. rubropunctum* as sect. *Pseudoleccinum* Smith & Thiers under *Boletus* (p. 313).

Sect. 2. *LECCINUM*. [*Versipelles* Fr. 1938 em. Konr. & Maubl. 1924-37, Sing. (1947)]. Hymenophore not yellow; stipe yellow at the base in certain specimens but not otherwise; context yellow at the base in many specimens but not otherwise; spore print olive umber brown to umber, or even cinnamon brown, e.gr. "Clove" (Maerz & Paul).

*Type species:* *L. aurantiacum* (Bull. ex St Aman) S.F. Gray.

**Subsection *Leccinum*.** Margin of the pileus projecting strongly as a sterile membrane, mostly breaking into segments. Veil present or absent; pores not strongly yellow; context yellow only in the base or tending to become yellowish there, mostly concolorous in stipe and pileus, or blue in the base (or staining blue); spore print brown without a distinct olive shade.

**Type species:** as in the section

1. Species with a veil.

*L. potteri* A.H. Smith, Thiers & Watling.

2. Species without a veil.

*L. aurantiacum* (Bull. ex St-Amans) S.F. Gray; *L. duriusculum* (Schulz. ap. Fr.) Sing. (sensu aut. nonn. e. gr. Watling\*) (*L. aurantiacum* var. *decipiens* Sing.); *L. quercinum* (Pilát) Green & Watling (*L. aurantiacum* var. *quercinum* Pilát); *L. vinaeopallidum* Smith, Thiers & Watling (*L. percandidum* ss. Sing.); *L. roseotinctum* Watling (*L. percandidum* (Vassilkov) Watling sensu Watling non Vassilkov); *L. testaceoscabrum* (Secr.) Sing.; *L. vulpinum* Watling. - Numerous additional species have been described from North America.

**Subsection *Scabra*** Smith, Thiers & Watling (1967). Projecting margin of the pileus insignificant or nil; veil none; pores not strongly yellow; context often discolored in the base of the stipe (yellow or blue); spore print brown; epicutis of the pileus all filamentous or mixed with shorter cells in chains but not formed by an epithelium.

**Type species:** *L. scabrum* (Bull. ex Fr.) S.F. Gray.

*L. snellii* Smith, Thiers & Watling; *L. oxydabile* (Sing.) Sing. (sensu Sing. 1967, Watling); *L. chalybaeum* Sing.; *L. holopus* (Rostk. in Sturm) Watling; *L. scabrum* (Bull. ex Fr.) S.F. Gray (with several forms and varieties); *L. rotundifoliae* (Sing.) Smith, Thiers & Watling (*L. scabrum* ssp. *rotundifoliae* (Sing.) Sing.). - Numerous additional species have been described in North America and Europe.

**Subsection *Albella*** Smith, Thiers & Watling (1967). Differing from subsection *Scabra* in an epithelial epicutis of the pileus.

**Type species:** *L. albellum* (Peck) Sing.

*L. albellum* (Peck) Sing. (with f. *epiphaeum* Sing.); *L. griseum* (Quél.) Sing. (*L. carpinum* (R. Schulz) Moser in Gams).

**Sect. 3. ROSEOSCABRA** Sing. (1947). Differs from the preceding section in even deeper (chrome) yellow base and, mainly, in the color of the spore print which is "Vassar tan" to "marron glacé", when dehydrated "tanbark" to "terrapin" or reaching "burnt almond" to "Tuscan tan" (Maerz & Paul).

\*The type of *B. duriusculus* does not exist in Budapest (Bohus in litt.); consequently, in view of the different interpretations, it may be better to consider *B. duriusculus* a nomen dubium. However, since no other species has been described in Europe which fits Schulzer's plate better, I accept Watling's interpretation as long as this species is not considered a variety of *L. aurantiacum* which is extremely close to *L. duriusculum* sensu Watling.

*Type species: L. chromapes* (Frost) Sing.

*L. chromapes* (Frost) Sing.

Sect. 4. *EXIMIA* Sing. (1973). Differs from the preceding section in inconstantly and then vaguely yellowish base and more variable spore color (mostly from "vinaceous buff" to "Argus brown", after dehydration near "Roods brown" Ridgway), not olive, but sometimes reaching "ferruginous".

*Type species: L. eximium* (Peck) Sing.

*L. eximium* (Peck) Sing. (*Tylopilus*, Sing., *B. robustus* Frost); a subspecies or closely related microspecies associated with *Quercus* has smaller spores.

## 220. XANTHOCONIUM Sing.

*Mycologia* 36: 361. 1944.

*Type species: X. stramineum* (Murr.) Sing.

*Characters:* Pileus not scrobiculate but often spotted, not bluing with NH<sub>3</sub>; hymenophore consisting of medium long, white to yellow tubes with small pores, the latter concolorous, plainly adnate or adnexed, or more frequently depressed around the apex of the stipe; spores in print "antique brown", "raw sienna", "mars yellow" or "Sudan brown" to "Argus brown" (Ridgway), or "Antique bronze", "burnished gold", "chipmonk" (Maerz & Paul), often more yellowish in thin layer, and more dull fuscous where they were in contact with the carpophore, bright golden under the microscope, cylindric to rod-shaped (Pl. 77,8), or fusoid-cylindric and always narrow, smooth, with thin, often pseudoamyloid walls; cystidia present in the tubes and on the pores, often with pseudoamyloid granulation (in *X. affine*), hymenophoral trama truly bilateral-divergent of the *Boletus*-subtype; stipe equal or ventricose, rather thick, glabrous but under a lens finely pruinose from dermatocystidia, subsMOOTH or smooth, solid; context white, unchanging, mild. On the ground in woods but not specific for coniferous or frondose trees, and found to be associated with either of these.

*Development of the carpophores:* Unknown.

*Area:* Temperate and subtropical North America.

*Limits:* Clearly separable from *Boletus* and *Tylopilus*. The color of the spores (not pink, not "Isabella color" or "chamois") and the white, mild, unchanging context correlated with non-reticulate, non-pustulate-flocculose stipe and slightly longer and narrower ( $Q = \pm 3 \pm 4$ ) spores separate *Xanthoconium* from *Tylopilus*. The color (in print and under the microscope) of the spores and the absence of known pigments separate it from *Boletus*; the shape of the spores may also serve as an auxiliary character. The yellow-spored species of the *Gyroporoideae* differ in having clamp connections, much shorter and less rusty colored spores which are not golden under the microscope. *Pulveroboletus viridis*, with a similar spore color

(ferruginous-ochraceous according to Corner 1972) has a glutinous stipe, becoming hollow, characters which are not encountered in *Xanthoconium*.

**State of knowledge:** Two species are known to the present author.

**Practical importance:** Both species are edible. They may have some potential importance in forestry since they are mycorrhizal, as far as field observations can indicate.

## SPECIES

*X. stramineum* (Murr.) Sing. (*Gyroporus*, Murr.); *X. affine* (Peck) Sing. (*Boletus*, Peck); apparently also *X. purpureum* Snell & Dick.

### 221. VELOPORPHYRELLUS Gomez & Sing.

*Brinesia* 22: 293. 1984.

**Type species:** *V. pantoleucus* Gomez & Sing.

**Characters:** Differs from *Porphyrellus* in absence of pigments (excepting the spores) and absence of enclosures in the completely hyaline, inamyloid cystidia, furthermore by the presence of a true veil which is non-gelatinous in all parts, membranous, not floccose-arachnoid; epicutis of the pileus trichodermial; hyphae without clamp connections. The absence of the pigments is relative insofar as the trama of the pileus becomes a very pale burgundy red on bruising. Pseudoamyloid spores are found among some weakly or not pseudoamyloid ones, all cyanophilous, smooth under the light microscope and not longer than 13.5  $\mu\text{m}$  in the type (and only) species.

**Development of the carpophores:** Apparently primary angiocarp; details not studied.

**Area:** Neotropical-montane, thus far only from Costa Rican *Quercus-Magnolia* forests above 1800 m alt.

**Limits:** The genus is closest to *Porphyrellus*, *Tylopilus*, and *Fistulinella*, differing by the cystidial characters and the characteristic veil from the first two genera, and from the last by the absence of gelatinization in all covering layers and slightly smaller spores as well as by the characteristics of the veil. *Austroboletus* has non-smooth spores.

**State of knowledge:** Only one species is known.

**Practical importance:** Unknown. The ecology of the species suggests that it is ectomycorrhizal with oak, but there is no anatomical or experimental proof.

## SPECIES

*V. pantoleucus* Gomez & Sing.

*Les Bolets*, p. 99. 1931; em.

Type species: *Boletus porphyrosporus* Fr.

Syn.: *Phaeoporus* Bat., *Bolets*, p. 11. 1908, non Schrötter (1888).

*Boletus* subgenus *Porphyrosporus* Smotlacha, *Monogr. Cesk. h. Hrib.*, p. 31. 1911.

*Tylopilus* subgenus *Porphyrellus* (Gilbert) Smith & Thiers, *Bol. Mich.* p. 94. 1971.

**Characters:** Pileus subvelutinous, velutinous, tomentose, or subtomentose, not viscid, dark or dusky colored; hymenophore pallid to cream gray or grayish brown; spore print "warm sepia", or tending to "wood brown" to "chestnut", or "benzo brown" (Ridgway); spores usually large, all with a  $Q > 1.5$ , smooth or rarely weakly ornamented, often or always  $\pm$  pseudoamyloid (said to be amyloid in one species), well pigmented; stipe neither scabrous nor viscid, evelate, mostly  $\pm$  concolorous with the pileus, more rarely at first pallid, smooth or somewhat rugulose or partly reticulate; context slowly discoloring, to gray, blue, brown or olive, by autoxidation; taste mild; cystidia often with pigmented and/or pseudoamyloid internal body; hyphae without clamp connections; hymenophoral trama of the *Boletus*-type; epicutis a trichodermium or trichodermial palisade, or almost hymeniform; KOH on pileus and/or context mostly positive with a distinct red or vinaceous component, eventually, or if applied after autoxidation, brown; NH<sub>3</sub> on fresh pileus not bluing. Ectomycorrhizal mostly with conifers and Fagales. Temperate perhaps also in tropics. No known pigments have been isolated or demonstrated in the carpophores.

**Development of the carpophores:** Unknown, probably all gymnocarpous.

**Area:** North temperate.

**Limits:** The genus is obviously closest to *Tylopilus* and *Austroboletus* but should, in my opinion be separated from the former generically since it has a number of characters (not only the spore color both in print and under the microscope) including chemical ones which separate it from all known species of *Tylopilus*. The spores are rather uniformly shaped (elongate) and colored (with a deeper colored and often thicker wall and frequently reaching larger size than those of *Tylopilus*). The genus consists of a number of closely related species which form a natural unit with a defined area much more reduced than that of *Tylopilus*. *Porphyrellus* differs from *Veloporphyrillus* in the constant absence of a veil, the presence of pigmented or pseudoamyloid material in the cystidia, and in the constant presence of pigments in the carpophore. In *Boletochaete* the spores are much smaller and shorter, the pseudocystidia soon become coscinoid, and the context is bitter; besides, this is a palaeotropical genus which *Porphyrellus* is not. *Fistulinella* has gelatinized covering layers and hyphae and colorless inamyloid cystidia.

**State of knowledge:** The Porphyrelli have been subdivided by Wolfe (1979) into two sections, *Porphyrellus* and (with one species) *Truncatosporus*. The truncate apex of the spores in boletes has not been proved to be a supraspecific character and occurs also in some spores of the type of *P. sordidus* (FH portion). The amyloidity of the

spores of the type species of this section has not been positively confirmed in the type nor has it been confirmed by me in those cases where it was mentioned by Smith. Consequently, the section *Truncatosporus* is not recognized here. The specific taxonomy of *Porphyrellus* is difficult, especially in North America where more species occur than in Europe and the various taxa are very close to each other. A key has nevertheless been published by Wolfe (1979) which may be helpful. The present author is well acquainted with four species.

**Practical importance:** At least two species of *Porphyrellus* are edible but not very valuable as food since the taste is not always rewarding. There are no poisonous species known. *P. porphyrosporus* and *P. pseudoscaber* are undoubtedly ectomycorrhizal, and the other species probably so.

## SPECIES

*P. porphyrosporus* (Fr.) Gilbert; *P. fumosipes* (Peck) Snell (*P. pseudoscaber* ssp. *cyanocinctus* Sing.; *Tylopilus cyanotinctus* Smith & Thiers); *P. pseudoscaber* (Secr.) Sing. (*P. pseudoscaber* var. *fuligineus* (Fr.) Sing.; *B. porphyrosporus* var. *minor* Bat.); *P. sordidus* (Frost) Snell; obviously also *Boletus nebulosus* Peck (but almost certainly a form of *P. pseudoscaber*); *B. olivaceobrunneus* Zeller & Bailey in Zeller (but generally taken to be a form of *P. pseudoscaber* or *P. porphyrosporus*); apparently also *P. amylosporus* A.H. Smith, *Boletus umbrosus* Atk., *Tylopilus pacificus* Wolfe and *T. snellii* Wolfe, also *T. brunneus* McNabb; perhaps *Austroboletus olivaceus* Sing. and *P. heterospermus* Heim & Perreau.

## 223. TYLOPILUS Karst.

*Rev. Myc.* 3: 16. 1881.

**Type species:** *T. felleus* (Bull. ex Fr.) Karst.

**Syn.:** *Rhodoporus* (Quél.) Bot., *Bolets* p. 11. 1908.

*Rhodobolites* G. Beck, *Zeitschr. f. Pilzk.* 2: 146. 1923.

*Leucogyroporus* Snell, *Mycologia* 34: 408. 1942.

**Characters:** Pileus subglabrous to tomentose, dry or almost so, cuticle of diverse structures, even sometimes cellular; hymenophore light colored or pallid at least when young, usually depressed around the stipe, at least at maturity; pores small, not discolored at the pore mouths except by autoxidation when injured; spore print ranging from a sordid pinkish flesh color to dull flesh ocher, wood brown, deep ferruginous brown, etc. ("Light russet vinaceous", "russet vinaceous", "fawn color", "army brown", between "wood brown" and "fawn color", "pinkish cinnamon" with a shade of "fawn color", "vinaceous fawn", "cream buff", "Isabella color" or "chamois" without an olive shade, "amber brown", etc. All these colors are indicated in Ridgway terms), often becoming dirtier or paler after prolonged preservation in the herbarium, pale melleous to melleous-subhyaline, or brownish-pallid to stramineous under the microscope, variable in shape, smooth, thin walled, generally not over 15.5  $\mu\text{m}^*$  long; castidia usually well-developed, gene-

\*except for occasional giant spores in a few species. Larger spores make a species suspect to belong to *Leccinum*, *Fistulinella*, or *Austroboletus*.

rally internally pigmented or with a pigmented or pseudoamyloid internal body and thus contrasting with the hyaline basidia; hymenophoral trama truly bilateral-divergent of the *Boletus* subtype; stipe either naked or covered with a palisade of hairs or dermatocystidia, often with a hymenium containing basidia in the reticulate portion of the stipe (these portions rather extensive in some species; context white or whitish or at least never extensively yellow, unchanging or turning pink, gray, lilac, brown on exposure, only exceptionally bluing, mild or bitter (not strongly acid or peppery). On the ground or (rarely on rotten wood, in the neighborhood of trees in woods and forests, generally forming obligatory ectomycorrhiza. Pigments generally different from those now known in *Boletus* as also in no. 220-226.

*Development of carpophores:* Apparently gymnocarpous.

*Area:* In the area of ectotrophic forests.

*Limits:* See under *Xanthoconium*, *Porphyrellus* and *Fistulinella*.

*State of knowledge:* 25 species are here recognized.

*Practical importance:* Some species are edible; the bitter ones may spoil a mushroom meal because of their taste which does not disappear in cooking, and some of these are even considered mildly poisonous by some authors. Since all species are obligatorily ectomycorrhizal, they may become important for the forester.

## SPECIES

Sect. 1. *TYLOPILUS* (*Fellei* Sing.). Context unchanging by autoxidation, rarely weakly bluing or eventually weakly reddened; spore print pinkish, e. gr. "French beige", "rose beige" Ridgway, or "pheasant testaceous" or "Formosa" Maerz & Paul; stipe often reticulate but glabrous, at least macroscopically, or subtomentose; spores ± elongate. Surface of pileus not bluing with NH<sub>4</sub>OH. - Ectomycorrhiza with Pinaceae and Fagales.

*Type species:* *T. felleus* (Bull. ex Fr.) Karst.

*T. roadsiae* (Murr.) Murr.; *T. minor* Sing.; *T. felleus* (Bull. ex Fr.) Karst.; *T. plumbeoviolaceus* (Snell) Snell; *T. lividobrunneus* Sing.; *T. nicaraguensis* Sing. & Ivory in Sing., Araujo & Ivory; *T. hondurensis* Sing. & Ivory in Sing., Araujo & Ivory; *T. neofelleus* Hongo.

*Note:* *T. formosus* Stevenson (context unchanging; spores "sayal brown" to "wood brown", stipe finely granular to furfuraceous) seems intermediate between sect. 1 and 2.

Sect. 2. *OXYDABILES* Sing. (1947). Differing from section 1 in the context turning pink, reddish, purplish, grayish red, avellaneous to brown or lilac when bruised, sometimes eventually black; spore print as above or slightly more pinkish gray-brown or "chamois" (Ridgway) to "Isabella color"; stipe either reticulated or not, but if so, generally also beset by small furfuraceous-pustulate flocculose punctations, or velutinous; NH<sub>3</sub> reaction not blue (or, in some species unknown, and then sect. 3 must be compared). Ectomycorrhiza mostly with Fagales.

*Type species: T. tabacinus* (Peck) Sing.

1. Spores decidedly elongated; epicutis with few or no isodiametric cells.

*T. tabacinus* (Peck) Sing. (with several varieties\*); *T. pachycephalus* (Mass.) Sing. (*Boletus alboater* Schwein. sensu Corner non Schwein.; *T. nigricans* (Pat. & Baker) Sing.); *T. sanctaerosae* Sing.; *T. alboater* (Schwein.) Murr.; *T. peralbidus* (Snell & Beardslee) Murr.; *t. appalachiensis* Sing.; *T. ferrugineus* (Frost) Sing.; *T. indecisus* (Peck) Murr.; *T. subpunctipes* (Peck) Smith & Thiers; *T. guanacastensis* Sing. in Sing., Araujo & Ivory; *T. alutaceo umbrinus* Hongo.

2. Spores elongated or short; epicutis or erect chains consisting mainly of isodiametric and subisodiametric cells.

*T. veluticeps* (Pat. & Baker) Sing.; *P. vinosobrunneus* Hongo; possibly here *Porphyrellus niger* Heinemann & Goos.

3. Spores decidedly short (5)-6.5-10.5-(11)  $\times$  3.7-5  $\mu\text{m}$ , mostly 6.5-8.5  $\times$  3.7-5  $\mu\text{m}$ , mostly 6.5-8.5  $\times$  4-4.8  $\mu\text{m}$  ( $Q = 1.3-2.2$ ); epicutis a hyphous trichodermium.

*T. balloui* (Peck) Sing.; perhaps also *T. otsuensis* Hongo.

Sect. 3. *ARENARII* Sing. \*\*. Differing from sect. 2 in a strong blue reaction of all (fresh) surfaces with NH<sub>4</sub>OH and KOH; spores elongate ( $Q > 2.2$  in mature spores), pigments violet on pileus and reticulation of stipe. Ectomycorrhiza with leguminous (Caesalpinoideae) and sapotaceous trees. Tropical.

*Type species: T. arenarius* Sing.

*T. arenarius* Sing. in Sing.; Araujo & Ivory; obviously also *T. beelii* Heinemann & Goos.

Sect. 4. *POTAMOGETONES* Sing. (1978). Spores short (all or in their majority with  $Q = 1.5-1.8$ , sometimes with a minority with  $Q = 2.2-2.7$ ) without suprahilar depression or applanation; NH<sub>4</sub>OH reaction blue on the pileus and stipe but often covered up by a thick tomentose-velutinous covering of both in youth; taste mostly bitter; context unchanging when bruised. Ectomycorrhiza with *Swartzia* and *Aldina* (Caesalpiniaceae) in Amazonia.

*T. potamogeton* Sing. with varieties.

## 224. BOLETOCHAETE Sing.

*Mycologia* 36: 358. 1944.

*Type species: Boletus spinifer* Pat. & Baker.

*Characters:* Pileus with a subepithelial or trichodermial-palisadic epicutis; pores small and much like those *Boletus*, at first white or whitish, adnate to deeply depressed around the stipe; hymenophoral trama of the *Boletus*-subtype; spores pale

\*The reticulation of the stipe and the incrustation of the pileus epicutis cell develop in the course of the individual development of the carpophores as was observed by me on Costa Rican material.

\*\*sect. nov. Sporis elongatis; carpophori superficie ammoniaci ope caerulescente.

cinnamon pink or pale ochraceous cream (Corner), i.e. print colored as in *Tylopilus*; spores inamyloid, small (less than 8  $\mu\text{m}$  long) and ellipsoid (Q less than 2, mostly  $\pm$  1.5); cystidia few, mostly in the form of pseudocystidia without contents, but pseudocystidia numerous and when mature becoming distinctly coscinoid, the walls thin to irregularly thickened becoming bistratous and 0.5-1.5  $\mu\text{m}$  thick, clavate and ventricose to awl shaped, pigmented (dark ferruginous, olive, fulvous brown, or melleous), metachromatic in toluidin blue and cresyl blue (external wall - blue, internal walls red); stipe variable in shape, often attenuated downwards or bulbous, neither scabrous nor reticulate but slightly pruinose to scurfy, central, solid. Context  $\pm$  bitter; hyphae without clamp connections, moderately and late gelatinizing (carpophores of the slow-growing, long-lived type).

*Development of the carpophores:* Gymnocalypous (?), cf. Corner (1972) p. 173, 32; Singer (1981), p. 284-285; Watling (1985).

*Area:* Paleotropical.

*Limits:* The genus is related to *Xanthoconium* and *Tylopilus* but differs from both in spore and cystidial characters. The  $\pm$  bitter taste, slow development and paleotropical distribution are also characteristic.

*State of knowledge:* Only two species are known at present.

*Practical importance:* Not known. Ectomycorrhizal relationships not yet demonstrated.

## SPECIES

*B. spinifer* (Pat. & Baker) Sing.; *B. bicolor* (Mass.) Sing.\*

### 225. FISTULINELLA Henn.

*Engl. Bot. Jahrb. 30: 43. 1901.*

*Type species:* *Fistulinella staudtii* Henn.

*Syn.:* *Ixechinus* Heim, *Rev. Myc.* 4: 20. 1939 ex Heim, *ibid.* 30: 233. 1966.  
*Mucilopilus* Wolfe, *Mycotaxon* 10: 117. 1979.

*Characters:* Pileus with an epicutis in form of a trichodermium or cutis, ixotrichodermium or ixocutis, the epicutis and/or hypodermium strongly gelatinized or becoming so in the course of development, surface of pileus at first glabrous or with strictly applicate superficial to innate fibrils, or subtomentose to tomentose, often scrobiculate; hymenophore tubular, with small to medium (to 0.65 mm diam.) concolorous pores, subisodiametric, even circular, to somewhat irregular and angular, often at different levels or with denticulate edges, initially pallid or whitish; spore print between vinaceous buff and fawn or "terrapin" or paler than "army br" to "pencil wood" or "sonora" (M&P); spores elongated, 9.5-22  $\mu\text{m}$  long, smooth, some

\*c.n. (= *Boletus bicolor* Mass., *Kew Bull.* for 1909: 205. 1909 non al.).

or all weakly to distinctly pseudoamyloid; cystidia hyaline, without colored or pseudoamyloid internal bodies or pigments or only some with weakly yellowish, at times weakly pseudoamyloid inside-bodies or granulation; stipe usually rather thin, never bulbous, somewhat widened or attenuated towards the base, or equal, glutinous, viscid, or dry, glabrous and smooth, or with slightly pustulate-scurfy surface, more rarely with reticulation, white or pink or buff; rarely darker or bright stained, reticulations, if present, waxy to viscid, veil none. Context mild to very slightly bitterish, unchanging on exposure; hyphae without clamp connections, hymenophoral trama of the *Boletus* type, the lateral stratum strongly gelatinized so that in most species the single tubes separate in liquid preparations, and in some species the individual pores are recognizable even in dried material (as in *Fistulina*). Basal mycelium white, more rarely yellow. Thermophilous.

*Development of the carpophores:* Unknown.

*Area:* In the Western hemisphere from warm temperate and subtropical to tropical zones reaching from South Carolina to Mexico and the West Indies, Venezuela, Brazil (Amazonia); also in Africa from Cameroon to Madagascar; also in New Zealand; Japan (southern Honshu).

*Limits:* The genus is most closely related to *Tylopilus* from which it differs in the gelatinization of the covering of the pileus and often also the stipe, the mostly thinner stipe and often large spores, the absence of pseudocystidia\* and, in section *Fistulinella*, the more striking separation of the tubes in liquids, also the less fleshy, thinner pilei and stipes. While all species of *Tylopilus* are ectotrophically mycorrhizal, this is at least doubtful for several species of sect. *Fistulinella* and merely probable although not proven for sect. *Scrobiculati*.

It appears that all species have smooth spores even in SEM replicas (Wolfe, Pegler & Young) so that *Autroboletus* is clearly separated by this character. However, the position of *Boletus rostrupii* which shows characteristics of both *Fistulinella* and *Austroboletus* (with a glutinous "annulus", pileus and stipe, but with strongly verruculose-spinulose spores), remains precarious. At present we follow Horak, Pegler & Young, and Wolfe, who consider the spore ornamentation decisive. *Fistulinella* is therefore characterized as being evelate. If future investigations on *F. mexicana* should show that the "vaina" of the stipe is a veil but that the spores are nevertheless SEM-smooth, it may still be advisable to redefine the limits between *Fistulinella* and *Austroboletus*. On the other hand the epicutis of more typical *Austroboleti* is often found to be gelatinizing or gelatinized from the beginning.

*State of knowledge:* 11 species are now recognized as belonging to *Fistulinella*. Wolfe (1984) has on the basis of a numerical approach, confirmed his original division of the genus into two sections, *Mucilopilus* and *Scrobiculati*. The result of the numerical method used by Wolfe is of course to a certain degree influenced by the inclusion of *B. viridis* (which is a *Pulveroboletus*, see Singer (1982) and by the omis-

\*The granular (protoplasmatic) contents of the cystidia shown by Heim for *Ixechinus majus* is apparently an artefact produced by the method of preservation, especially, in my experience, by prolonged action of the alcohol-formol used in conservation liquids.

sion of certain species and relevant data obtained by others so that neither the phytogeographical nor the morphological characterization of the two sections corresponds fully to the sum of data now available. Nevertheless, the two sections appear to be acceptable as shown below.

**Practical importance:** Unknown. Whether all or some species are ectomycorrhizal is at present very difficult to establish inasmuch as some are consistently lignicolous and none has thus far been proved to be obligatorily ectomycorrhizal.

## SPECIES

Sect. 1. *SCROBICULATI* (Sing. 1947, p. 95 as *Tylopilus* sect. *Scrobiculati*) Sing.; *Mucilopilus* sect. *Scrobiculati* (Sing.) Wolfe. Pileus at first dry, but an ixotrichodermium or ixocutis developing, appressed-fibrillose to tomentose at first, scrobiculate or not; stipe not glutinous nor viscid. Associated with *Quercus* or *Castanopsis* (ectomycorrhiza?). Species of the Northern Hemisphere.

*Type species:* *Tylopilus conicus* (Rav. apud Berk. & Curt.) Beardslee.

*F. conica* (Rav. apud Berk. & Curt.) Pegler & Young with var. *conica*, var. *belizensis* Sing. & Ivory in Sing., Araujo & Ivory, and var. *reticulata* (Wolfe); *F. nipponica* Nagasawa ined.

Sect. 2. *FISTULINELLA*. Pileus viscid to glutinous; stipe also often viscid to glutinous. Species associated with *Nothofagus*, Leguminosae, Sapotaceae, Leptospermaceae, perhaps not ectomycorrhizal; restricted to the tropical belt and the Southern Hemisphere.

*Type species:* *Fistulinella staudtii* Henn.

*F. staudtii* Henn.; *F. campinaranae* Sing.; *F. mexicana* Guzmán; *F. jamaicensis* (Murr.) Sing.; *F. venezuelae* (Sing. & Digilio) Sing.; *F. viscida* (McNabb) Sing.; *F. violaceispora* (Stevenson) Pegler & Young; *F. major* (Heim) Guzmán ("majus" Heim); *F. minor* (Heim) Guzmán ("minus" Heim); obviously also *Porphyrellus nothofagi* McNabb (*Mucilopilus*, Wolfe) and *F. gloeocarpa* Pegler.

## 226. AUSTROBOLETUS (Corner) Wolfe

*Bibl. Mycol.* 69: 64. 1979.

*Type species:* *Boletus dictyotus* (Boedijn) Corner.

*Syn.:* *Boletus* subgen. *Austroboletus* Corner, *Bol. Malaya* p. 76. 1972.

*Porphyrellus* sect. *Tristes* Sing., *Farlowia* 2: 115. 1945.

*Porphyrellus* sect. *Graciles* Sing., *ibid.* p. 119.

**Characters:** Pileus viscid or dry, mostly covered by a trichodermium or ixotrichodermium; spore print color varying from that of *Tylopilus* to that of *Porphyrellus* but mostly about "hazel" (R.) "vinaceous brown" (Kornerup & Wanscher), "oak"

(M&P), "Vandyke br" (M&P), "army brown", "Verona brown" reaching "warm sepia" (R.) in thick layers, sometimes becoming "Sudan brown" by dehydration; spores with variable ornamentations (often VI, I, XI) visible in the light microscope, more rarely appearing smooth in the light microscope but distinctly verruculose (SEM, e. gr. *A. niveus*), mostly decidedly elongated-fusoid, more rarely Q = ± 2, inamyloid to pseudoamyloid; cystidia generally without pigmented or pseudoamyloid internal bodies but setoid cystidia sometimes present at the pores; stipe glabrous or subglabrous (faintly punctate) to finely pustulate-furfuraceous and smooth to either almost scabrous or reticulate or longitudinally ridged, the reticulation frequently lacunose-alveolate, evelate or with a glutinous sheet ending up in a subapical glutinous, narrow annulus (*A. rostrupii*), or connecting with a wide sterile appendiculation of the pileus (*A. dictyotus*), but more often dry or (the reticulation) waxy; context unchanging, or variously discolored, even blackening at times, by autoxidation; taste mild or more rarely slightly bitter. No red KOH reaction on carpophores in fresh condition; no blue NH<sub>4</sub>OH reaction on surfaces in fresh condition. Hyphae without clamp connections, inamyloid. Ectomycorrhiza not consistently formed.

*Development of the carpophores:* Probably mostly gymnocarpous, but Corner's (1972) figures 25-26 suggest primary angiocarpy in the type species (pilangiocarpous and stipitocarpous according to Watling (1985).

*Area:* Few species in the north-temperate and south temperate zone, many species in the neo- and paleotropics.

*Limits:* As Wolfe has shown (*Bibl. Myc.* 69. 1979), *Austroboletus* is generically different from *Porphyrellus*. As for its separation from *Fistulinella*, it appears that the limits of the latter (see there), basically restricted to the presence or absence of an ornamentation, are still in need of further studies, so are the spores of those species (including the type species of *Fistulinella*) where EM studies are still wanting. If indeed the spores of *F. staudtii*, appearing quite smooth under oil immersion, were EM-ornamented, it would appear that both genera are too close to be maintained and might be combined whereby *Austroboletus* would become a synonym of *Fistulinella*.

*State of knowledge:* Wolfe (l.c.) has proposed two sections of *Austroboletus*, based on the ornamentation type of the spores. Since this subdivision is based exclusively on characters not available for many species since it has to be checked on EM replicas, and as long as a considerable variation in spore ornamentation can be observed in a single species (see Corner 1972, fig. 24) we cannot at present accept any subdivisions even though the growing number of species belonging here (I have personally studied 12 species) will in the future require the recognition of at least two sections.

*Practical importance:* At least one (and possibly all) species are edible but of minor practical importance. Some species seem to be ectomycorrhizal but in most cases the mycorrhizal association is insufficiently explored, and apparently not uniform or consistent in all species.

## SPECIES

### 1. Stipe conspicuously lacunose-alveolate-reticulate.

*A. dictyotus* (Boedijn) Wolfe; *A. subvirens* (Hongo) Wolfe; *A. subflavidus* (Murr.) Wolfe; *A. malaccensis* (Pat. & Baker) Wolfe; *A. cookei* (Sacc. & Syd.) Wolfe; *A. fusisporus* (Kawamura ex Imazeki & Hongo) Wolfe; obviously also *A. niveus* (McNabb) Wolfe; *A. novaezelandiae* (McNabb) Wolfe; *A. mucosus* (Corner) perhaps also *A. rostrupii* (Syd. & Syd.) Horak (Wolfe); and *Boletus rubiicolor* Corner.

### 2. Stipe shallowly reticulated and longitudinally ridged, or ridged only.

*A. gracilis* (Peck) Wolfe with var. *gracilis* and var. *laevipes* (Peck) Wolfe.

### 3. Stipe not reticulate and not (or only slightly) ridged, rarely velutinous-subreticulate.

*A. tristis* (Pat. & Baker) Wolfe; *A. longipes* (Mass.) Wolfe\*; *A. festivus* (Sing.) Wolfe; *A. amazoniensis* Wolfe & Sing. ined.; *A. rionegrensis* (Sing. & Araujo) Sing. in Sing.; Araujo & Ivory; perhaps *A. heterospermus* (Heim & Perreau) Sing. in Sing., Araujo & Ivory and *A. olivaceus* Sing. in Sing., Araujo & Ivory, both possibly to *Porphyrellus*.

## Subfamily Strobilomycetoideae (Gilbert) Snell

*Mycologia* 33: 422. 1941 ("Strobilomycetaceae").

*Type genus: Strobilomyces* Berk.

Spores generally short, subglobose to ellipsoid, ornamented, in print without an olivaceous tinge but darker fuliginous than in other Bolete genera with ornamented spores; hyphae without clamp connections; hymenophoral trama of the *Boletus*-type; pileus usually fleshy, squamose to squarrose or areolate with soft scales or warty, woolly-fibrous; veil present, not glutinous but dry; pigments responsible for the color changes of the context (reddening, blackening) specific (tyrosine - Dopa - melanines); a red KOH reaction present in the species checked. Apparently ectomycorrhizal.

Only one genus known.

## 227. STROBILOMYCES Berk.

*Decades Fungi*, Hooker's Journ. Bot. 3: 77. 1851.

*Type species: S. strobilaceus* (Scop. ex Fr.) Berk.

\**A. tristis* is considered a young stage of *A. longipes* by Corner (1972, 1980) but I agree with Wolfe that the type specimens (FH, K) suggest specific differences inasmuch as the dermatocystidioid terminal cells of the epicutis and especially the stipe covering are also different, the latter subvesiculose to vesiculose 15-27.5 × 9-10 µm in *A. tristis*.

*Syn.*: *Eriocorys* Quél., *Enchiridion* p. 163. 1886.

*Afroboletus* Pegler & Young, *Trans. Brit. Myc. Soc.* 76: 130. 1981.

**Characters:** Those of the subfamily.

**Development of the carpophores:** Probably metavelangiocarpous and stipitocarpous.

**Area:** Most common and rich in species in the subtropical and tropical belt of Southern Asia and Africa, but also represented by one to two species in North America, Tropical America, Northern and Eastern Asia, and Australia.

**Limits:** The genus, and with it the subfamily, is most closely related to *Austroboletus* but amply different by spore characters and chemotaxonomically.

Sect. *Pterospori* has spore ornamentations which remind one somewhat of *Boletellus* but the latter genus is not truly related as has been confirmed by pigment studies, and the family Strobilomycetaceae, as defined by Gilbert and formerly by myself had therefore to be abandoned.

Sect. *Pterospori* has been separated from *Strobilomyces* by Pegler & Young (1981) because of the spore ornamentation type and the supposed restriction of the species belonging in it to tropical Africa. They named this genus *Afroboletus*. I agree that this is a good, natural taxon but do not believe that it deserves generic rank. The aspect, colors, spore print color, brown to chocolate brown or purple brown in thin, nearly or quite black in thick layers are shared with sect. *Strobilomyces*. The 'plage' in sect. *Strobilomyces* remains the only character supporting even a sectional subdivision of the genus, but it seems to be replaced, in sect. *Pterospori*, by a basal thickened rim. Arpin & Kühner (1977) rightly stress the frequent reddening and constant blackening (tyrosine - Dopa - melanines) as characteristic of *Strobilomyces*. This phenomenon holds sections *Strobilomyces* and *Pterospori* (*Afroboletus*) together.

Pegler & Young's well-documented observations which could be extended to other, particularly controversial species like *B. nanus*, are undoubtedly very valuable for the taxonomist as are those by Wolfe. Nevertheless, they cannot be a basis for a 'natural' classification, which, by definition, has to take all available characters into account.

Neither is the distribution of the species of sect. *Pterospori* restricted to tropical Africa. A neotropical species has been discovered in Amazonian Brazil (*S. pauper*).

**State of knowledge:** The species of *Strobilomyces* are comparatively well known. Ten species are completely known (except, for some of them, the chemical color reactions) to me.

**Practical importance:** *S. floccopus* is edible but has little importance as food. Ecological observations seem to indicate that (perhaps all) species of *Strobilomyces* are ectomycorrhizal.

## SPECIES

Sect. 1. *STROBILOMYCES* (*Genuini* Sing. 1945). Spores either smooth or with imbedded short spines or warts, or with ridges or reticulations (Pl. 73, 1-2, 6); ornamentation low or absent in a suprahilar region.

*Type species:* *S. floccopus* (Vahl in Fl. Dan. ex Fr.) Karst.

*S. floccopus* (Vahl in Fl. Dan. ex Fr.) Karst. [*S. strobilaceus* (Scop. ex Fr.) Berk.]; *S. confusus* Sing.; *S. velutipes* Cooke & Massee; *S. nigricans* Berk.; *S. echinatus* Beeli; *S. polypyramis* Hooker fil. apud. Berk.; *S. montosus* Berk.; obviously also *S. annulatus* Corner, *S. foveatus* Corner, *S. mollis* Corner, and probably *S. mirandus* Corner.

Sect. 2. *PTEROSPORI* Sing. (1945). Spores winged-ribbed from the hilar end to the apex (Pl. 73, 8).

*Type species:* *S. pterosporus* Sing.

*S. costatisporus* (Beeli) Gilbert; *S. pterosporus* Sing.; *S. pauper* Sing. in Sing., Araujo & Ivory; and probably another species from the Belgian Congo indicated by Gilbert; probably also *Boletus ater* Henn. and *Strobilomyces luteolus* Heinemann.

### Subordo RUSSULINEAE Sing.\*

*Syn.:* *Russulales* Kreisel, Grundzüge, p. 163. 1969 (without Latin diagnosis), as order.

*Asterosporales* Heim (invalid), p.p., as "série générale évolutive".

*Bondarzewiales* Jülich, Bibl. Myc. 85: 344. 1981 (as order).

Spores with an amyloseous ornamentation; hyphae without clamp connections (excepting one species of *Lactarius* where the clamped hyphae are restricted to the lower part of the stipe); hymenophoral trama with spherocysts and/or laticiferous hyphae present; trama with monomitic or dimitic structure and, if hymenophore lamellate, at least partially containing spherocysts (heteromerous), if hymenophore tubular, dimitic; carpophores stipitate, with primary or secondary angiocarpous or gymnocarpous. Saprophytes, or parasites, or ectotroph formers.

Endocarpous (gastroid) forms are here excluded. These enter the suborder Hydnangiineae with the families Hadnangiaceae, Elasmomycetaceae, Hybogastraceae and Octavianinaceae, some of these not formally described, some possibly products of gastromycetation (?), all with apobasidia.

*Type family:* Russulaceae Roze.

\*subordo nov. Sporis ornamentatione amylacea gaudentibus; hyphis defibulatis (una specie Lactarii excepta); tramate (si dimiticum est) homoiomero, ceterum ut minime e parte heteromero. Familia typica: Russulaceae.

## KEY TO THE FAMILIES

A. Hymenophore tubular; trama nowhere heterotromerous, dimitic; root parasites.

BONDARZEWIACEAE, p. 803

A. Hymenophore generally lamellate; trama at least in some part (pileus) heteromerous. Root and leaf parasites, saprophytes, or (especially in the temperate forms) ectotrophically mycorrhizal.

RUSSULACEAE, p. 805

## BONDARZEWIACEAE Kotlaba & Pouzar

Cesk. Mykologie 11: 163. 1957.

Type (and only) genus: *Bondarzewia* Sing.

**Characters:** Pileus and stipe tough-fleshy to almost leathery-fleshy, often lactescent with a white, milk-like, often abundant latex when bruised; usually densely gregarious to polypilos-aggregated; hyphal system (in contrast to Russulaceae which is monomitic) dimitic with generative and skeletal hyphae which (as in some Polyporaceae) show transition towards the ligative type; conducting elements (at least in some species) present, even numerous in the form of laticiferous hyphae; in parts of the carpophore the skeletal hyphae absent or late in forming, but thick-walled hyphae present in most sections of all species; clamp connections absent in all types of hyphae, and all hyphae inamyloid; no gelatinization anywhere; spherocysts absent in the trama; spores like those of the Russulaceae, viz. short, hyaline to pale citrine, white or whitish in print, with an amylaceous (amyloid) ornamentation, cyanophilic, with smaller punctuation over a suprahilar discoid surface but mostly without a distinct plage and generally without a suprahilar amyloid spot, basidia normal; cystidia none but lactocystidia (extensions of the laticiferous ducts in the hymenial layer) often numerous; veil none; hymenophore tubular; carpophores large; taste often acrid or astringent. On the roots of living trees, on living and dead tree trunks, mostly on Fagales and conifers, parasitic on the roots.

**Limits:** The family was originally conceived to include also the Hericiaceae and Amylariaceae but these are basically different in many ways and are not considered to be either closely related or belonging to the Agaricales. *Bondarzewia* and the Bondarzewiaceae are, however, considered to belong to the Agaricales because of their anatomical similarity with the Russulaceae especially *Lactarius* sect. *Panuoides* which is corroborated if the gastroid genus *Hybogaster* (see also p. 846) is taken into consideration. This comes in every regard so close to *Bondarzewia* that it is at times difficult to distinguish it from *Bondarzewia guaiotecasensis* (descriptions of the two species see Singer, *Mycologia* 45: 884. 1953 and *Sydotwia* 17: 13. 1964, respectively) when seen at a distance at its natural habitat.

*Lactarius igapoensis*, a root parasite, has the subiculum and lower part of the stipe consisting of dimitic trama, otherwise rather reduced heteromerous trama, a white latex, eccentric stipe, all characters that approach *Bondarzewia*.

The spores of *Bondarzewia* with inconsistent suprahilar plage and absence of an amyloid suprahilar spot differ slightly from those of *Russula*, sect. *Russula* but

*Bondarzewia*-like spores can be observed in many species of *Russula* and *Lactarius*. The structure of the spore wall is practically the same in Russulaceae and Bondarzewiaceae when studied in EM sections (cf. Antoine-Benson, Thèse Univ. Claude-Bernard, Lyon 1972; Keller, Thèse Univ. Neuchâtel 1974). Ornamentation ridges running towards the hilar end exist not only in *Bondarzewia* spores but likewise in Russulaceae and representatives of the asterogastraceous series.

The inclusion in Bondarzewiaceae of an aphyllophoraceous genus near *Fomitopsis* is not accepted here, not only because its inclusion would extend the limits of the Agaricales as here defined, but also because real affinity between *Heterobasidion annosum* and *Bondarzewia montana* has not been demonstrated. Stalpers (*Taxon* 28: 414-416. 1979) although correctly stating that the spores of both species are ornamented and amyloid, neglects the fact that they are otherwise quite different and that laticiferous hyphae are absent in the *Fomitopsis*-like polypores. His 5 point "support" for inclusion of *Heterobasidion* in the Bondarzewiaceae (aside from Echinodontiaceae and Amylariaceae) is correct as far as the facts are concerned, but with these similarities as well as with the redescription of Bondarzewiaceae sensu Stalpers the affinity of the groups included is not proved, and the 5 points and definition of the family allow inclusion of many other Basidiomycetes quite unrelated to *Bondarzewia* while the demonstrably related ones, like *Lactarius igapoensis* and *Hybogaster giganteus* Sing. are by his diagnosis, omitted.

A careful study of the taxa involved and the arguments given proves that the Bondarzewiaceae sensu stricto are a family of Russulineae, and that their similarity with polypores is only superficial (cf. *Nov. Hedw.* 40: 435-446. 1984\*), see also p. 108-109.

## 228. BONDARZEWIA Sing.

*Rev. Mycol.* 5: 4. 1940.

*Type species:* *B. montana* (Fr.) Sing.

*Characters:* Those of the family.

*Development of the carpophores:* Probably gymnocarpous, not studied in detail.

*Area:* North temperate zone, south temperate zone (*Nothofagus* area), possibly also in southern Brazil.

*Limits:* These are discussed under Bondarzewiaceae, p. 111.

*State of knowledge:* Three species are now known in *Bondarzewia*, each specialized with regard to host requirements.

*Practical importance:* All three species are parasitic and destructive and are therefore important in plant pathology and silviculture. *B. berkeleyi* contains the alkaloid hordenine (West et al., *Lloydia* 37: 633. 1974; Lee & al. *Lloydia* 38: 450-452. 1975).

\*Proof corrections were not taken into account; p. 441 read "rear portion" not "reapportion"; p. 445, 3rd line read "-merous" not "-tropic", p. 446, last line before "Literature" read "amylaceous" not "amyloid"; pl. 2-4 are reproduced too white (see description).

## SPECIES

*B. montana* (Quel.) Sing.; *B. berkeleyi* (Fr.) Bond. & Sing.; *B. guattecasensis* (Henn.) J.E. Wright apud Sing. (*B. perniciosa* Sing.).

## RUSSULACEAE Roze

*Bull. Soc. Bot. Fr.* 23: 51. 1876 (nom. nud. ut Russulariées); l.c. p. 110; R. Maire, *Recherches* p. 131. 1902 (ut Russulacées); Lotsy, *Vorträge* p. 708. 1907.

Type genus: *Russula* Pers. ex Gray.

Syn.: *Lactariaceae* Gäumann, *Vergleich. Morph. Pilze* p. 529. 1926.

**Characters:** Stipe usually fleshy, pileus often vividly colored; cuticle varying in structure, often covered by a layer of velar origin, the cuticle proper consisting of up to three layers (epicutis, hypodermium, and subcutis) and beneath it often an infrahypodermial layer present; hymenophore ordinarily lamellate, lamellae either normally alternating with the lamellulae (didymous, tridymous) or lamellulae few and irregularly interspersed or entirely absent and then all lamellae equal, usually very brittle (or lactescent), free to decurrent, crowded to distant, thick to moderately thin, wedge-shaped; basidia normal 4-spored, rarely 2-spored; true cystidia rarely present except at the edges of the lamellae (cystidiole-like cheilocystidia, rarely well differentiated cheilocystidia); macrocystidia (Pl. 21, 4) commonly present (but in some species replaced by another type of pleurocystidia or pseudocystidia: gloeo-cystidia); hymenophoral trama subregular to irregular or intermixed, in *Russula* mostly intermixed, with numerous spherocysts, in *Lactarius* more often without spherocyst-nests; spore print white to deep ochraceous-yellow or pinkish cream, the color usually characteristic for sections, subsections or species\*; spores (Pl. 14, 1) under the microscope hyaline to yellowish, usually short-ellipsoid to globose or sub-globose, more rarely oblong to oblong-subcylindric, never quite smooth (except when very young) but always beset with an exosporial (but see p. 56) ornamentation which is strongly amyloid (containing amyロン according to Locquin and therefore perhaps better called amylaceous); ornamentation of type I, II, III, IV, V, VI, VII, VIII, or exceptionally in a minority of spores - IX); heterotrophic, with a less ornamented suprahilar region or a distinct, delimited amyloid hilar spot or disc, (weakly) cyanophilic at least in the amylaceous covering zone, hilum of the nodulose type; stipe usually central, and fleshy, usually solid at first, later often stuffed or

\*For the Russulaceae a special color chart has been devised in order to differentiate between the various spore colors ranging from pure white to deep ochraceous. This can be found in Crawshay (1930). Color citations "A", "B", etc. refer to his plate. A more recent chart with more defined shades can be found in Romagnesi (1967). Neither this nor J. Schäffer's reproduction (1933) of Crawshay's plate agree completely with the originals so that the quotation given by these authors do not always match precisely the published plates. This is an unavoidable difficulty caused by reproduction problems. When Romagnesi's categories are quoted (Ia, b, IIa, b, etc.) the reference is to the plate as published. Blum has recommended a scale of dehydrated spore prints, but as in the Boletaceae, our quotations if not otherwise indicated, are based on the fresh spore print before dehydration.

hollow or more rarely hollow from the beginning; with annular veil or without veil (more often evelate), without pseudosclerotium, mostly without rhizomorphs; context (pl. 29) white, or colored, often containing a latex, consisting, at least in some part of the carpophore, of nests of spherocysts and connective hyphae (heteromerous), all these elements inamyloid and non-pseudoamyloid, always without clamp connections in the hyphae of the trama of the pileus and mostly also of the stipe (only in *Lactarius quercum* the hyphae of the lower part of the stipe are clamp-bearing); gloeovessels, lactiferous hyphae or oleiferous hyphae present. Mostly on the ground in ectotrophic forests and plantations, rarely on living or dead plant material, mostly obligatorily ectomycorrhizal, fewer species facultatively ectomycorrhizal or non-mycorrhizal, rarely parasitic on *Cormophyta*.

**Limits:** The heteromerous trama without clamp connections in the pileus, and the amyloid spores with distinct ornamentation are sufficient to distinguish this family from all others. The Bondarzewiaceae are closest but differ in some respect, most obviously by the tubular hymenophore and the absence of spherocysts.

#### KEY TO THE GENERA

- A. Latex absent; pigments mostly intracellular, very rarely intraparietal or intercellular; Wood's light and polarized light causing a certain degree of luminescence; trama of the lamellae usually with spherocysts in the half nearer the edge; lamellae equal or intermixed. 209. *Russula*, p. 806
- A. Latex present (except for older, dry specimens), either forming droplets of watery or milky-opaque consistency, or merely moistening the surface of freshly bruised tissue; pigment often only intraparietal, and intercellular pigment also occurring; trama of the lamellae mostly (except for certain primitive groups) not containing spherocysts, at least in the half closer to the edge; lamellae practically always intermixed. 210. *Lactarius*, p. 829

#### 229. RUSSULA Pers. ex S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 618. 1821.

*Type species:* *R. emetica* (Schaeff. ex Fr.) Pers. ex S.F. Gray.

*Syn.:* *Omphalia* Pers. ex S.F. Gray, l.c. p. 611\*, non *Omphalea* L. (1759).  
*Russulina* Schröter in Cohn, *Kryptog.-fl. Schlesien* 33(1): 550. 1889.  
*Phaeohygrocybe* Henn., *Engler's Bot. Jahrb.* 30: 50. 1901.  
*Lactarelis* Earle, *Bull. N.Y. Bot. Gard.* 5: 409. 1909.  
*Dixophyllum* Earle, l.c. p. 410.  
*Omphalomyces* Batt. ex Earle, l.c. p. 410.

\*Donk (1962) selects as lectotype of *Omphalia*: *Agaricus tardus* "Pers. [S.F. Gray]" which is *A. cyathiformis* Bull. (1786) sensu Bull. (1792) = *Agricus cyathiformis* Fr. While the equation given is obviously correct (cf. Singer, *Persoonia* 2: 48. 1961), the method of typification is not. In view of Art. 7, note 7 and the "Guide for the determination of types", paragraph 3f, *O. adusta* must be chosen. A reference to a preliminary, nameless pre-Frisean mention as source of Gray's genus is pointless in view of the fact that *A. adustus*, the selection first made by authors independent of the first-species-rule, is actually in the section *Omphalia* Pers. 1801, p. 459 where it enters the group *Maiores*.

It is quite another question whether *Omphalius* Roussel ex Earle and *Omphalia* Pers. ex S.F. Gray should have the same type. Evidently they cannot, because Earle excluded *A. adusta*. This makes *Omphalius* Roussel ex Earle a different taxon irrespectively of what could or should have been done about *Omphalia* Pers. ex Gray. It is a superfluous name (Art. 63).

**Characters:** Those of the family. Latex absent (see also key above). Pl. 14, 1; 21, 4; 29; 39.

**Development of the carpophores:** Gymnocalycous in the majority of the temperate species; in other, especially more tropical species pilangiocarpous, or mixangiocarpous then pilangiocarpous; pileostipitocarpic (Reijnders 1963, 1976 for *R. anthracina*, *ochroleuca*, *fragilis*); "hemiangiocarpous" (probably monovelangiocarpous) in some tropical species (in particular *R. batistae*), according to Singer & Araujo.

**Area:** Almost cosmopolitan (but absent from tree-less regions excepting those where dwarf ectotrophs exist), in the temperate and frigid zones generally very well represented within the ectotroph area but also in the tropical forest, often forming cicatrizing mycorrhiza.

**Limits:** The limits have been expressed in the key above. The delimitation is practically never difficult because the presence or absence of the latex respectively laticiferous hyphae is sufficiently sharp a character to rely upon in fresh material since it is always constant. However, in dried material, one is pressed for secondary, anatomical or external characters, and for physical and chemical means of differentiation between *Russula* and *Lactarius*. Even with dried material, there are only three groups of species where the two genera seem to "touch" each other, and these are the *Albati-Plorantes* complex, the *Archaeinae-Lactariopsis* complex and the *Archaeinae-Polysphaerophori* complex. In all cases, secondary characters can be found ad hoc in order to distinguish herbarium specimens of these sections, e. gr. in the case of *R. delica* and related forms, one can rely on the presence of spherocysts in the hymenophoral trama in order to be sure that *Lactarius deceptivus* or related species are not misinterpreted as Russulaceae.

*Macowanites* (Elasmomycetaceae - Gasteromycetes) is often strikingly similar to young or deformed Russulaceae, but differs in never shedding a spore print. Here we cannot agree with Pegler & Young's (1979) inclusion of *Arcangelia*, *Cystangium* and *Macowanites* in the family Russulaceae since in these genera the spores are not, physiologically, ballistopores even though the majority (but typically not all) of the basidia and sterigmata have (already or still - whatever your evolutionary theory) the configuration called "agaricoid", i.e. half-sickle-shaped, curved-inward sterigmata and the carpophores are not always pileate nor the hymenophore consistently lamellate. In the herbarium, the revision of dried specimens does not furnish the data decisive for a decision whether a species is physiologically and ecologically a Gasteromycete or an "agaric". If the specimens are quite mature, it helps some-

The argument that Gray's *Arrangement* is a flora and did therefore not contain other species than the ones enumerated by him is without basis in the Code and contradicted by the fact that other species of sect. *Omphalia* pers. are quite common in England and were enumerated by Gray but none belongs in *Omphalina* or goes beyond the delimitation given by Persoon; in fact such species as were generally accepted in the Saccardo scheme (based on Fries, *Hymenomycetes*) under *Omphalia* later on, are found in the genus *Mycena*. Gray's genus *Omphalia* is a mixture or *Russula*, *Clitocybe*, *Pseudolitocybe*, *Paxillus*, *Laccaria*, *Lentinellus*, and *Camarophyllus*.

The question of the correct lectotypification of *Omphalia* (Pers.) ex S.F. Gray is, besides, an academic one since *Omphalia* has been and should be treated as a later homonym of *Omphalea* L. (1759).

times to search for discharged spores on the sterile surfaces but this method of determining the basidia as autobasidia is not always dependable. Furthermore, the spores of Russulaceae sensu str. do not always have a plage and even less an amyloid spot in the suprahilar region. The "so-called punctum lacrymans" can, with any degree of certainty, be established only on living material.

Consequently, even though I was among the first to recognize the affinity between the genera of the Hydnangiaceae-Elasmomycetaceae with *Russula* and *Lactarius*, (cf. *Beih. Bot. Central.* 49 II: 231. 1932), we must not forget that if there is such a group or taxon as Gasteromycetes, *Cystangium* and *Macowanites*\* belong to it no less than the Hybogasteraceae. The fact that opinions among those who combine gastroid taxa with agaricoid taxa are divided with regard to the kind and number of taxa which should be taken out of the "Gasteromycetes proper" is proof enough that, to say the least, the time for splitting up the Gasteromycetes has not yet come.

*State of knowledge:* *Russula* belongs to the best-known genera in spite of the fact that more data on both fresh and dried material are necessary here than in most other fleshy fungi excepting perhaps some boletaceous genera and *Lactarius*. The nomenclature of the sections, subsections, and species is by no means as well settled as the descriptive data for most species. Unfortunately, each author of modern treatments follows his own preferences as far as names are concerned - an attitude which has shown undoubtedly a deterrent effect on the non-specialist who is inclined - unjustly in this particular case - to generalize from the stage of nomenclature on the general stage of knowledge in *Russula*.

However, there is no genus in the Agaricales where more species have been studied anatomically and chemically, in addition to exact macroscopical descriptions available in world monographs (which, however, are somewhat predominantly concerned with European material); there is no genus where more type specimens and authentic material has been critically revised in the light of modern methods. There is no genus on which more effort has been spent by local and traveling specialists even in such regions as China, Madagascar, Florida, North Africa, Caucasus, and South and Central America from Mexico to Tierra del Fuego.

It is possible that the continued study of the structure of epicutis and subcutis will eventually reveal the presence of certain subtypes that might advantageously be used for the distinction of species and subsections. The pseudocystidia of *Russula polyphylla* and *R. mutabilis* stained throughout their interior a deep and rich blue when dyed with cresyl blue, and sulfoformol did not stain but rather left them hyaline or pale yellow (in *R. polyphylla*). In contrast to this, sulfoformol stains the pseudocystidia of *R. emetica* deep brown, and cresyl blue does not stain the contents of the bodies. The latter have been called macrocystidia by Romagnesi, and the pseudocystidia of *R. polyphylla* are, according to the definition, gloeocystidia.

\*There is apparently some convergence of character combinations in typical species of *Macowanites* on one hand and Russulaceae, retarded or diseased, which are fully mature but produce no spore print. This convergence makes it extremely difficult to define the limits of the genus on a morphological-anatomical basis alone. Similar problems, all involving the phenomenon of gastromycetization, are found in *Gastroboletus* and *Thaxterogaster*. By the simple expedient of combining the gastroid and agaricoid genera and families, no deeper insight into the taxonomy or evolution of Basidiomycetes can be gained.

It is also possible that more chemical reactions will be discovered. But as a whole the character of *Russula* have been evaluated to a very high degree, and the distinction of species is not too difficult after enough experience has been accumulated, and all data are patiently collected. Pigment analysis will undoubtedly be an invaluable help for the taxonomist in a genus where much emphasis is on color. Unfortunately, the study of the pigmentation is not very advanced in *Russula* in spite of very interesting contributions which have been summarized by Arpin & Fiasson in Petersen, *Evol. Higher Basidiom.*, p. 81-83. 1971 and Eugster, *Zeitschr. f. Pilzk.* 39: 79-92. 1973. The beautiful and characteristic red pigments in the cuticle of many species which has allegedly given the name to the genus, the "Russula-Rot" of Zellner was re-studied by Eugster who found them to be copper complexes with remarkably high Cu-content; they are usually mixtures.

Even in the best monographic work on European Russulaceae by Romagnesi, the degree of gelatinization and extension, if any, of the layer we call subcutis (between epicutis and hypodermium) is not fully described; only in the latest work it has found sufficient attention. Heim's (1937) example of describing and illustrating the presence or absence of an amyloid dot in the suprahilar region of the spores has likewise not been heeded by all later workers, but seems to be importance for the definition of sections.

Partial and regional monographs have been published by several modern authors, e. gr. Singer (1932), J. Schäffer (1933), Heim (1937), Shaffer (1962, 1964), and Romagnesi's most detailed and very valuable work (1967), not to mention earlier basic contributions by R. Maire (1907, 1910) Melzer & Zvára (1927) and Melzer (1945) and recent regional treatments by Singer for Catalonia (1982) and Singer & Araujo for the neotropical lowlands (1983).

As for the choice of the correct name, the author has, as in the other chapters of the present book, attempted to adhere to the International Rules more rigidly than ever, including the choice of the sectional and subsectional names, even in cases where this attitude may be criticized as not conforming to tradition. Friesian names are admitted in a certain sense even if this interpretation cannot be proved as being correct, if no serious discrepancies in the opinions of the authors exist; and if they do exist, the name was adopted only if the dissenting author is believed to be wrong for some serious reasons. As important and serious, the author considers such dissenting opinions as have been published by modern specialists of the genus or by authors whose views have greatly influenced the literature. Even so, the decision in certain cases cannot be considered as entirely due to nomenclatorial reasoning but must necessarily be partly based on the personal views of the author in regard to the reliability of certain data published in original descriptions, in regard to the probability of a certain interpretation in view of the occurrence of a species in certain regions and in view of the value attributed to published or unpublished pictures which are or are not in complete agreement with the diagnoses.

The Sydney-rules (International Code 1983) have aggravated the difficulties of naming even some of the most common European species of *Russula* (see also *Mycotaxon* 18: 191-200. 1983). In the present work, we uniformly disregard the new wording of Art. 13.

The author recognized now 317 fully known species in the genus.

**Practical importance:** Russulas are used for food in many countries, especially by the Slavic population of Eastern Europe. Few species are valuable for anything but pickling or salting. *R. cyanoxantha* is one of the exceptions. Nevertheless, *Russulae* are often found in the markets of Western Europe. One species is considered as probably slightly poisonous, viz. *R. foetens*. But in Japan, *R. subnigricans* is very poisonous (Hongo 1960). The presence of muscarine and epimuscarin has been confirmed for *R. emetica* by Stadelmann et al. (*Helv. Chim. Act.* 59: 24-33. 1976).

Many *Russulae* are considered as a good source for certain enzymes, especially tyrosinase (*R. delica* and others).

The *Russulae* occurring in the temperate zones must be considered as obligatory mycorrhizal fungi forming obligatory ectotrophic mycorrhiza with forest trees of various families, mostly conifers (*Pinus*, *Picea*, *Abies*, *Larix*, *Pseudotsuga*, *Tsuga*, etc.) and Fagales and Salicales, but they are also found to form mycorrhiza with *Tilia*, Leguminosae, and Sapotaceae, Nyctaginaceae and Polygonaceae. It seems that most species live normally under the conditions of mutual symbiosis; consequently they may be of some importance in forestry.

Since 1958 (see Singer, *Mycopathologia et Mycologia applicata* 9: 275-278, pl. II. 1958; *Lilloa* 30: 126-127. 1960) we know that Russulas are among the fungi used by the natives of New Guinea to provoke what is known as the "Wahgi River frenzies". The first species known with certainty to be involved was *Russula nondorbingi* but *Russula wahgiensis* may also be used. Heim indicates aside from six boletes several white Russulas similar to *R. nondorbingi* (Heim, *Les champignons associés à la folie des Kuma. Cahiers du Pacifique* 7: 1-64, pl. I-XX. 1965). The importance now given to psychotropic substances derived from fungi may also be justified in the case of *Russulae*.

## SPECIES

Sect. 1. *PELLICULARIAE* Heim. Margin of pileus pectinate to very deeply folded-sulcate on adult and thin-fleshed pilei (not merely tuberculate-sulcate or shallowly sulcate), sometimes striped paler at the same time, the rim of the margin acute or subacute, never rounded-obtuse; veil sometimes present; spore print white to cream (Ia, Ib, IIa, Romagnesi chart); development of the carpophores often velangiocarpous or secondarily angiocarpous; ectomycorrhiza either not formed or only facultatively, or, if obligatory, in association with leguminous trees (mostly Caesalpinioideae), Sapotaceae, Nyctaginaceae, Polygonaceae rather than with Fagales or conifers. Macrocytidia or cystidia not thick-walled unless spores without a suprahilar amyloid spot. Tropical.

*Type species: R. annulata* Heim.

Subsect. *Epitheliosae* Sing. in Sing. & Araujo (1983). Epiutis - an epithelium; gelatinous subcutis absent; yellow stains, veil and red to violet pigments absent. Neotropical.

*Type species: R. epitheliosa* Sing. in Sing. & Araujo.

*R. epitheliosa* Sing. in Sing. & Araujo.

Subsect. *Guayarenses* Sing. in Sing. & Araujo (1983). Epicutis - a Virescens structure; gelatinous subcutis present; yellow stains, annular veil, and red to violet pigments absent; cystidia with thickened walls, these eventually 1-1.5  $\mu\text{m}$  thick in most cystidia, contents yellowish, amorphous, banded or granular, rarely absent. Tropical.

*Type species: R. guayarensis* Sing. in Sing. & Araujo.

*R. guayarensis* Sing. in Sing. & Araujo; *R. eburneoareolata* Hongo.

Subsect. *Radicantes* Heim (1938). Extensive yellow surface on stipe and/or yellow areas in context present, or surfaces stain strongly yellow or orange; cystidia not with thickened walls; taste not acrid but often unpleasant; annular veil present, or stipe tomentose-fibrillose; spores with rather isolated warts (ornamentation type VI, V (IV). Paleotropical. - Oxidase reactions weak (Heim).

*Type species: R. radicans* Heim.

*R. radicans* Heim; *R. aureotacta* Heim; perhaps also *R. xylophila* Beeli.

Subsect. *Heliochrominae* Heim (1938). Differs from the preceding subsection only in constant absence of an annulus, mild taste, glabrous or grossly pruinose stipe, and ornamentation type not being VI, V. Tropical. - Oxidase reactions (in *R. heliochroma*) strong (Heim). In some species pectination of pileus weak or forming late.

*Type species: R. heliochroma* Heim.

*R. theissenii* Rick; *R. zenkeri* (Henn.) Sing.; *R. heliochroma* Heim.

Subsect. *Discopodinae* Heim (1938). Carpophores not staining orange, with strong oxidase reactions; veil annular or absent; pectination of the pileus wide and strong; spore print Ia, or between Ia and Ib (Romagnesi chart); spore ornamentation of type I, II, IIIa, usually many spores suborthotropic; subiculum in form of a basal disc or bulblet often differentiated from the stipe; gelatinous subcutis well developed, epicutis hyphous, but sometimes with cystidiform terminal cells or some kind of Virescens-structure but then (in contrast with subsect. *Guayarenses*) hymenial cystidia decidedly thin-walled; taste mild. Tropical.

*Type species: R. annulata* Heim.

*R. annulata* Heim; *R. puiggarii* (Speg.) Sing. (*Clitocybe*, Speg.; *R. brasiliensis* Sing.; *R. hygrophytica* Pegler in Pegler & Sing.); *R. neodiscopoda* Sing.

Subsect. *Diversicolores* Sing. in Sing. & Araujo (1983). Carpophores not brightly colored (no bright yellow, orange, red, purple, violet pigments, but pileus fuscous or olivaceous to avellaneous, more rarely with some pink tones mixed in) and not staining yellow or orange, but stipe and context tending to become concolorous with the pileus or gray in age and on drying; macrocystidia absent (cystidia not bluing in sulfovannilin, thin-walled). Veil none. Neotropical.

*Type species: R. diversicolor* Pegler in Pegler & Sing.

*R. verna* Sing. in Sing. & Araujo; *R. venezuelae* Sing.; *R. diversicolor* Pegler in Pegler & Sing.

Subsect. *Pluviales* Sing. in Sing. & Araujo (1938). Differs from the preceding section in unchanging surfaces and context, presence or macrocystidia, and red, lilac, purple, or violet pigments. Development (in *R. pluvialis*) secondarily angiocarpous. Tropical.

*Type species: R. pluvialis* Sing. in Sing. & Araujo.

*R. pluvialis* Sing. in Sing. & Araujo; *R. leguminosarum* Sing. in Sing. & Araujo; apparently also *R. carmesina* Heim.

Subsect. *Batistinae* Sing. in Sing. & Araujo (1983). Differs from the preceding subsections in cream colored (near Romagnesi IIa) spore print, in young carpophores acrid taste and the presence of a fugacious thin-membranous veil; development of the carpophores velangiocarpous; context unchanging but tending, as the lamellae, to become cinereous, but stipe tending to become ochraceous-orange (but unlike the *Radicantes*, the spore print is deeper cream and the spores have an ornamentation type II, IIIa, IIIb). Neotropical.

*Type species: R. batistae* Sing.

*R. batistae* Sing.

Sect. 2. *DELICOARCHAEAE* Sing. in Sing. & Araujo (1983). Margin of the pileus smooth, acute; lamellae intermixed, almost didymous; spore print white or pale colored; spores without a suprahilar amyloid spot; context rather hard and rigid, unchanging; appearance much like that of section 3, *Plorantes*; gelatinous subcutis absent; veil absent; macrocystidia present, cheilocystidia differentiated, both thinwalled; dermatopseudocystidia present on the pileus (epicutis). Ectotrophic mycorrhiza apparently not formed. Neotropical, possibly pantropical, possibly also in France, Africa, Japan.

*Type species: R. auvarum* Sing.

*R. auvarum* Sing.; perhaps here *R. immaculata* (Beeli) Sing., *R. subfragilis* Rick; *R. camarophylla* Romagn.; *R. japonica* Hongo.

Sect. 2a. *ARCHAEINAE* (Heim). Differs from sect. 2 in complete absence of cystidia. Palaeotropical. This section is based on Heim's description of *Compactae* subsect. *Archaeinae* Heim (1937, no Latin) and is unknown to me. Type species: *R. archaea* Heim. If macrocystidia can be demonstrated in Heim's species, sect. 2 and 2a might be combined under the name *Archaeinae* Romagnesi which has priority (*Bull. Soc. Linn. Lyon.* 37: 105. 1968). Romagnesi indicates *R. camarophylla* Romagn., but this has macrocystidia.

Sect. 3. *PLORANTES* Bat. ex Sing. (1982). Margin of pileus smooth, acute; lamellae intermixed, often didymous; spore print usually pale colored (Ib or IIa to IIc, rarely between Ia and Ib, according to Romagnesi in one species IVb, often with a

tinge of D (Crawshay); spore with a distinct suprahilar amyloid spot; context rather hard and rigid, unchanging or slightly staining pink especially in the lamellae; appearance often reminding one of *Lactarius* sect. *Albati*; pigments often restricted to a yellowish or pale tan colored discoloration appearing in mature pilei, sometimes in a blue zone at the apex of the stipe or in somewhat glaucescent lamellae; gelatinous subcutis present or absent; macrocystidia present and in most species bluing in sulfovanillin; dermatopseudocystidia usually present. Ectotrophically mycorrhizal. Widespread but apparently absent in the tropical lowlands.

*Type species:* *R. delica* Fr.

*R. delica* Fr., *R. brevipes* Peck; *R. chloroides* (Krombh.) Bres.; *R. delicula* Rom. (these species probably varieties of *R. delica*); *R. pseudodelica* Lange; *R. idroboi* Sing.; *R. fuegiana* Sing.; *R. vesicatoria* Burl.; according to Romagnesi also *R. flavigpora* (Blum in Romagnesi) Romagnesi (with spore print IVb, Romagnesi).

Sect. 4. *CRASSOTUNICATAE* (Sing.) Sing. (st. n. = Ingratae subsect. *Crassotunicatinae* Sing., *Sydotwia* 11: 157. 1957). Differs from sect. 2, *Delicoarchaeae*, in browning context, anilin and FeSO<sub>4</sub> reaction (red, respectively green), from sect. 3, *Plorantes*, also in the absence of an amyloid suprahilar spot on the spores, and white spore print (Ia to between Ia and Ib, but darkening in the herbarium eventually to IIa). Apparently ectomycorrhizal. North American, perhaps also tropical African.

*Type species:* *R. crassotunicata* Sing.

*R. crassotunicata* Sing.; *R. compacta* Frost & Peck apud Peck; probably also *R. liberiensis* Sing. (FeSO<sub>4</sub> reaction and odor not known, but thick-walled hyphae present).

Sect. 5. *COMPACTAE* Fr. (1838). Margin of pileus smooth, acute; lamellae intermixed, generally polydymous; spore print white (Ia, Romagnesi); spores decidedly heterotropic, without a suprahilar amyloid spot; context firm, at first hard, often becoming pink on bruising, also often blackening, or at least becoming grayish in age or on drying; basidia rather elongate (more so than in most other sections) and epicutis not sharply separated from the epicutis or subcutis. Ectotrophically mycorrhizal but often unspecialized. More common in the north temperate than in the south temperate and tropical zones.

*Type species:* *R. nigricans* (Bull. ex Fr.).

*R. nigricans* (Bull. ex) Fr.; *R. dissimilans* Shaff. (probably a subspecies of *R. nigricans*); *R. lateriticola* (Heim) Sing.; *R. adusto-densifolia* (Secr.) Sing. (*Agaricus adustus densifolius* Secr., Myc. Suisse 1: 476. 1833); *R. acrifolia* Romagnesi (*R. densifolia* var. *caucasica* Sing.); *R. albonigra* (Krombh.) Fr. (*R. michiganensis* Shaffer; ?*R. densissima* (J. Schäffer) Moeller in Hertz ex Romagnesi (see *Collect. Botan.* 13: 672. 1982); *R. subnigricans* Hongo; *R. purpureonigra* Petch; *R. albonigroides* Sing.; *R. eccentrica* Peck (cf. Bills, *Brittonia* 37: 360. 1985) unless to *Ingratae*.

Sect. 6. *PACHYCYSTIDES* Sing. in Sing. & Araujo (1983). Margin of pileus

smooth, acute; lamellae not didymous or polydymous; spore print Ia or between Ia and Ib (Romagnesi-chart); spores decidedly heterotrophic, with a distinct suprahilar amyloid spot; context not hard and rigid, unchanging, not acrid; macrocystidia absent in hymenium and on sterile surfaces absent; cystidia very numerous, very voluminous (to 24  $\mu\text{m}$  broad), often glassy-refrangent; epicutis - a trichodermium formed by ciliate dermatocystidia and hyphal ends; gelatinous subcutis differentiated or not; pigments initially practically none, later some yellowing or (on pileus) graying observed. Probably ectomycorrhizal with Leguminosae or *Glycoxyilon*, or Fagales. Mainly tropical; also in Japan.

*Type species:* *R. pachycystis* Sing. in Sing. & Araujo.

*R. pachycystis* Sing. in Sing. & Araujo; *R. nondorbingi* Sing.; *R. castanopsisidis* Hongo.

Sect. 7. *METACHROMATICAЕ* Sing. in Pegler & Sing. (1980). Margin of pileus not pectinate, acute; lamellae intermixed with lamellulae, sometimes didymous or tridymous; spore print white (Ia Romagnesi-chart); spores decidedly heterotrophic; with, rarely without a suprahilar amyloid spot; context not particularly hard and rigid, unchanging when bruised, mild or acrid; odor none or insignificant; macrocystidia numerous in the hymenium, these with thick (often  $> 1 \mu\text{m}$ ) metachromatic (in cresyl blue mounts) walls; gelatinous subcutis well developed; dermatopseudocystidia present on the epicutis of the pileus and the stipe; pigments, if present, yellow; probably ectomycorrhizal (e. gr. with polygonaceous, sapotaceous, and leguminous hosts). Neotropical.

*Type species:* *R. metachromatica* Sing.

*R. metachromatica* Sing.

Sect. 8. *DECOLORANTES* (R. Maire) Sing. (1926). Margin of the pileus not pectinate, obtuse; lamellae not di-, tri-, or polydymous but either  $\pm$  equal or with a few lamellulae intermixed; spore print variable; odor often of camembert; taste mild or somewhat acrid; spores decidedly heterotrophic, with a suprahilar amyloid spot; context characteristically graying or blackening and often also staining pinkish or red, distinctly reddening with formalin (thus chemically similar to sect. *Compactae* and differing from the following sections). Widely distributed and apparently always ectomycorrhizal.

*Type species:* *R. decolorans* Fr.

Subsect. *Decolorantinae* Maire (1910, "Decolorantes"). Dermatopseudocystidia of the macrocystidial type present on the epicutis of the pileus, primordial hyphae very few or absent.

*Type species:* *R. decolorans* Fr.

*R. decolorans* Fr.; *R. gaminii* (Dupain) Sing.; *R. steinbachii* Cernohorsky & Sing. *R. consobrina* (Fr. ex Fr.) Fr.; *R. columbiana* Sing.; *R. subobscura* Murr.; *R. rufescens* Beardslee; *R. cinerascens* Beardslee; *R. subdensifolia* Murr.; *R. burkei* Burl.; *R. californiensis* Burl.

Subsect. *Vinosinae* Sing.\* Dermatopseudocystidia absent, but primordial hyphae numerous in the epicutis of the pileus.

Type species: *R. vinosa* Lindbl.

*R. vinosa* Lindbl.; *R. seperina* Dupain (if different from *R. vinosa*\*\*; *R. flava* Romell in Lönnergren; *R. magna* Beardslee; *R. subsericeonitens* Murr.; *R. nigrescentipes* Peck; *R. subdepressa* Peck; *R. columbiana* Sing.; *R. occidentalis* (Sing.) Sing.; possibly also *R. rubens* Heim ex Heim.

Sect. 8. *INGRATAE* Quél. (1888) em. Maire (1910), Heim (1937) non Melzer & Zvára (1927), J. Schäffer (1933). Margin of the pileus smooth to long-tubercular-sulcate, in some cases even pectinate, acute to subacute when young; lamellae all equal or intermixed with lamellulae or forked, but not didymous or tridymous; spore print varying, from white (Ia) to pale ocre (Ib to IIIa, Romagnesi-chart); spores decidedly heterotrophic, mostly with a suprahilar amyloid spot, more rarely without it; context not particularly hard and rigid but usually flexible to fragile when mature, mild to acrid, often with an unpleasant taste; macrocystidia generally present, often also gloeocystidial; rudiments of a veil often present but veil not connecting margin and stipe at any stage (except perhaps primordium?) as far as known; surface of pileus often darkening (brown) with KOH, never red, purple, violet, green; pigments often intraparietal or even incrusting. Widespread. Mostly ectomycorrhizal.

Type species: *R. foetens* Pers. ex Fr.

Subsect. *Fistulosinae* Heim ex Sing.\*\*\* Margin of the pileus smooth or short-sulcate, acute or subacute, surface of pileus covered with granular floccos or scales, often becoming areolate or pustulate-tuberculate, dry, the ornaments formed by ascendant or erect hyphae and dermtocystidia, these often somewhat thick-walled, mostly with intraparietal and/or incrusting pigment (yellowish to brownish), with a similar structure on the surface of the stipe, the epicutis elements often rising from sphaerocysts or directly from a gelatinized subcutis which, however, may be very shallow; color of pileus and stipe mostly partly or entirely brown or yellow to orange; context white or grayish or concolorous, mild or acrid; spores decidedly heterotrophic, without or with suprahilar amyloid spot; spore print white to cream or pale ocher (Ia-Ib to IIIa, Romagnesi-chart). Widespread. Formation of ectotrophic mycorrhiza probable but not demonstrated.

Type species: *R. fistulosa* (forme A) Heim.

*R. fistulosa* Heim; *R. balloui* Peck; *R. tennesseensis* Sing. (probably but a form or variety of *R. balloui*); *R. burlinghamiae* Sing.; *R. matoubensis* Pegler in Pegler & Sing.; *R. earlei* Peck; also: *R. tuberculosa* Heim and *R. hoehnelii* Sing.

\*Decorantes dermatopseudocystidiis pilei destitutis.

\*\*As for *R. seperina* see *Collectanea Botanica* 13: 673. 1982.

\*\*\*Pileo stipiteque granuloso-flocculoso vel squamuloso, saepe areolato vel pustulato-tuberculato. Typus: *R. fistulosa* Heim ex Heim, *Candollea* 7: 386. 1938.

Subsect. *Subvelatae* (Sing.) (sect. *Subvelatae* Sing., *Beih. Bot. Centralbl.* 49. II: 243. 1932). Differing from subsect. *Fistulosinae* by the fact that the pellicle proper is easily separable in the marginal region and is covered by pale yellowish to sulphureous or brownish yellow loosely attached fine flocculi consisting of hair-like hyphae which are smooth or partly incrusted and hyaline to yellow (by an intracellular pigment), tending to turn "Mars orange" (Ridgway) with KOH. These flocculi are considered veil relicts even though they were never seen to form an organ covering the lamellae at any stage. Spore print Ia to IIb (Romagnesi-chart); mycelium apparently ectomycorrhizal. Subtropical in Asia and America, in North America reaching Canada (*R. pulverulenta*), in Europe reaching France (*R. insignis*).

Type species: *R. subvelata* Sing.

*R. subvelata* Sing.; *R. pulverulenta* Peck; *R. mutabilis* Murr.; *R. insignis* Quél. (*R. "livescens* (Batsch) Quél. ss. Bres." Romagnesi non Batsch nec al.).

Subsect. *Foetentinae* Melzer & Zvára (1927) (incl. *Obtectae* Sing. 1948). Pileus glabrous (i.e. not with the covering described for subsection *Fistulosinae* and not with the superficial flocculi described for subsection Subsection *Subvelatae*), with mostly at maturity tuberculate-sulcate or ± pectinate margin which is acute or subacute; taste disagreeable or acrid, more rarely mild and not disagreeable; odor often of nitrobenzene, bitter almonds, or similar, or else of lemon, malt, iodoform, fish, camembert or spermatic, more rarely absent; not fruity as *R. queletii* (compote of pears) or *R. emetica*; color of the pileus ochraceous brown, rusty brown, dull yellowish to nearly pallid, or else gray, grayish fuliginous, umber, bister or pallid-sordid; stipe white or with the colors of the pileus, or violet to lilac, sometimes dark furfuraceous, region of basal mycelium sometimes discolored (red, yellow). Wide-spread, ectomycorrhizal.

Type species: *R. foetens* Pers. ex Fr.

Stirps *Granulata*. (Pileus surface scurfy-granular from innate granules; colors as in stirps *Foetens*; spore print cream; base of stipe discolored (rusty red to sordid lilac)).

*R. granulata* Peck (*R. obtecta* Sing.); *R. fragrantissima* Romagnesi.

Stirps *Foetens*. (Pileus yellowish-ochraceous-rusty brown, to rarely almost pallid; odor often of nitrobenzene, or similar.)

*R. foetens* Pers. ex Fr.; *R. laurocerasi* Melzer; *R. punctipes* Sing.; *R. deremensis* Henn.; *R. elastica* (Heim) Sing.; *R. ventricosipes* Peck; perhaps *R. consobrinoides* Heim; *R. lilacipes* Shear; obviously also *R. senecis* Imai and *R. illota* Romagnesi (but both probably = *R. punctipes* Sing.); also *R. ochrostraminea* Pegler in Pegler & Sing.; *R. mephitica* Pegler in Pegler & Sing.; obviously also *R. josserandii* Bertault.

Stirps *Pectinata*. (Pileus rarely colored as in stirps *Foetens*, but usually more grayish fuliginous, umber, bister, or pallid-sordid; odor of camembert, or fresh fish, of iodoform, or malt, or lemons, or spermatic.)

*R. pectinatoides* Peck; *R. pectinata* Fr. (*R. amoenolens* Romagnesi); *R. sororia* (Fr.) Romell (*R. consobrina* var. *sororia* Fr.); *R. quercusoleoidis* Sing. in Sing. & Araujo; *R. aosma* Sing.; *R. sororiicolor* Sing. in Sing. & Araujo (the latter, if white-spored, and possibly *R. aosma*, may be separated from this stirps).

Subsect. *Farinipedes* Sing.\* Differs from the preceding subsection, stirps *Foetens* (of which it has the colors) in the very numerous dermatopseudocystidia which strongly react blue in sulfovanillin, in fruity odor and white (Ia) spore print. It differs from subsection *Felleinae* in more sulcate, also more acute margin and intracellular pigments throughout. North temperate species, Caucasus and Himalaya.

Type species: *R. farinipes* Romell apud Britz.

*R. farinipes* Romell apud Britz.

Subsect. *Felleinae* Melzer & Zvára (1927). Pileus with at first  $\pm$  subacute, smooth eventually  $\pm$  sulcate, obtuse margin; context often tending to stramineous or grayish (in age), acrid; pigments, at least in many hyphae of the epicutis intraparietal; surface of pileus glabrous, stramineous, brass yellow, bright yellow in parts, often tending to melleous or entirely gilvous. Northern temperate species.

Type species: *R. fellea* (Fr.) Fr.

*R. fellea* (Fr.) Fr.; *R. simillima* Peck (probably but a form of *R. fellea*); *R. ochroleuca* Pers. ex Fr.

Sect. 9. *RIGIDAE* Fr. (1838) (*Heterophyllae* Fr. 1851; *Lilaceae* Konr. & Joss. 1935). Pileus pruinata all over (not merely with a detersible and very fugacious pruina at the extreme margin), subvelutinous to velutinous, subtomentose to tomentose, areolate, squamulose-rimulose, or scurfy to sericeous, more rarely glabrous; taste mild, bitter, moderately acrid in the young lamellae (and then margin at first sometimes acute), or strongly acrid (and then lamellae polydymous or regularly forked, or dermatopseudocystidia absent); formalin with context not reddening;  $\text{FeSO}_4$  with context negative, or green, or salmon color, or grayish pink to pinkish-gray-sordid (normal); spore print A, B, C, D, or E (Crawshay); cuticle of the pileus not darkening with KOH; context not becoming or staining yellow or yellowish brown unless it becomes olive green with  $\text{FeSO}_4$ ; spores distinctly heterotrophic, with suprahilar amyloid spot except in some species of some subsections (*Amoeninae*, *Virescentiae*). Ectomycorrhizal. Widespread (especially subsect. *Cyanoxanthinae*), otherwise temperate but occasionally observed in the tropical-montane zone in Fagales forest.

Type species: *R. lepida* Fr. (= *R. rosacea* (Pers. ex) S.F. Gray).

Subsect. *Cyanoxanthinae* Sing. (1932). Pigment nearly absent, or bright colored (violet, lilac, livid-vinaceous, green, pinkish-vinaceous, or often not abundant, and the pileus rather pale and somewhat multicolorous, or brown; cuticle glabrous, or sericeous, or scurfy; lamellae with numerous lamellulae or forked lamellae often

\*Subsect. nov. Sporis in cumulo albis; pigmentis flavidis vel brunneolis hyphas pilei haud incrustantibus; dermatopseudocystidiis in sulfovanillina caerulescentibus; pileo glabro vel subfurfuraceo aut rimuloso.

Typus: *R. farinipes* Rom. ex Britz.

interspersed in a more or less alternating manner, rather flexible and not brittle; FeSO<sub>4</sub> usually (unless spores oblong) almost negative with the context, or slightly grayish green; spore print A or B (Ia to IIa, Romagnesi, but if not Ia with a pinkish hue), margin of the pileus acute.

*Type species: R. cyanoxantha* (Schaeff. ex Schw.) Fr.

*R. cyanoxantha* [Schaeff. ex Krombl.] Fr., var. *cyanoxantha* [f. *cyanoxantha*, f. *peltereum* Sing., f. *lilacina* Britz., f. *pallida* Sing.\*], var. *variata* (Bann. apud Peck) Sing. (*R. variata* Bann. apud Peck); *R. heterospora* Beardslee; *R. cremoricolor* Earle; *R. albiduliformis* Murr.; *R. cremeolilacina* Pegler in Pegler & Sing. with var. *cremeolilacina* and var. *coccolobicola* Sing. in Sing. & Araujo (*R. littoralis* Pegler in Pegler & Sing.); *R. costaricensis* Sing. in Sing. & Araujo; *R. amnicola* Sing. in Sing. & Araujo; *R. nanella* Sing. in Sing. & Araujo; *R. heterochroa* Sing. in Sing. & Araujo; obviously also *R. cutefracta* Cooke sensu Romagn. (unless conspecific with *R. cyanoxantha*).

Subsect. *Schizoderminae* Sing. Pigment bright colored or dull; cuticle broken into small areolae, squamulose-rimulose; epicutis devoid of gloeo-vessels and macrocystidioleiferous hyphae, also devoid of spherocysts.

*Type species: R. schizoderma* Pat.

*R. schizoderma* Pat.; *R. septentrionalis* Sing.; *R. yunnanensis* Sing. with var. *pseudoviridella* Sing.; perhaps also *R. cinerella* Pat. and *R. coffeata* Perreau.

Subsect. *Polyphyllinae* Sing. Pigment of the pileus almost none, or if present, green; a scurfy upper layer of the cuticle consisting mainly of gloeo-vessels or macrocystidioleiferous hyphae; gelatinous subcutis present.

*Type species: R. polyphylla* Peck.

*R. polyphylla* Peck (*R. magnifica* Peck); *R. polycystis* Sing.; *R. viridella* Peck.

Subsect. *Lividinae* Melzer & Zvára (1927). Pileus with bright colored pigment but not bright red; margin subacute, the cuticle often receding from the extreme margin leaving the latter denudate; context never reacting normally (pinkish-gray-sordid) with FeSO<sub>4</sub> but either gray-green in part, or salmon color, never negative; taste perfectly mild; context not turning yellow or brown on bruising, odor not of trimethylamine; spore print white (A, A-B); epicutis with ciliate dermatocystidia (not blue in sulfovanillin), or hair-like.

*Type species: R. vesca* Fr.

*R. vesca* Fr.; *R. flocculosa* Burl.; *R. ferrotincta* Sing.; *R. rigida* Vel. ("R. livida Pers." Melzer & Zvára, non *Agaricus lividus* Pers. ex Schwein., Secr.); *R. furcata*

\*This form and f. *peltereum* sing. are identical with what Fries describes as *R. heterophylla* in 1838. His original *A. furcatus* var. *heterophyllus* Fr., the basionym, var. a, is based on *A. lacteus* Pers. which was later interpreted by Fries in full agreement with its original diagnosis, as *R. lactea* (Pers. ex) Fr., a good species of subsection *Lilaceinae* and recently rediscovered in Austria and Hungary. The recent interpretations of *R. heterophylla* as *R. furcata* ss. Ricken are without historical or nomenclatorial basis.

(Gmelin ex Fr.) Fr. sensu Ricken; *R. heterophylla* (Fr.) Fr. sensu J. Schäffer, Romagnesi, non Fr.).

Subsect. *Modestinae* Sing. (1957). Dermatamacrocystidia present; spores white, sometimes cream but not deeper than B (Crawshay) i.e. between Ib and Ia; FeSO<sub>4</sub> reaction always positive but variable; otherwise as *Lividinae*.

*R. brunneola* Burl.; *R. leucomodesta* Sing.; *R. modesta* Peck; *R. mustelina* Fr. FeSO<sub>4</sub> possibly *R. variegatula* Romagnesi.

Subsect. *Subcompactinae* Sing. (1932). Pileus with bright colored pigment but neither bright rose red, nor yellow, with subacute to almost obtuse margin, the latter rarely denudate; context most frequently reacting normally (pinkish-gray-sordid) with FeSO<sub>4</sub> but sometimes showing a more salmon reaction over part of the context, never negative or green; spore print B or C (C-D), not A nor D (i.e. Romagnesi IIa to IIIc or paler, if = IIa-IIIc, the glabrous forms belong in subsection *Subcompactinae* but most forms with scurfy-pruinose pileus; epicutis usually with some dermatopseudocystidia, or at least potentially so, sometimes with numerous dermatopseudocystidia and ciliate dermatocystidia at the same time but then the latter without a subcuticular layer of noticeably shortened and partly sub-isodiametric elements (in the latter case, if there are no dermatopseudocystidia - see *Virescentinae* and if there are dermatopseudocystidia - see *Modestinae*); taste usually not perfectly mild in young specimens (hymenophore slightly acrid when quite fresh), never bitter; pileus somewhat scurfy, or pruinose, or velutinous, or glabrous. Pigments in fresh specimens, water preparations of the cuticle of the pileus, characteristically granular, bluish black or olive and distinct (Romagnesi, Maire)\*.

Type species: *R. subcompacta* Britz. sensu Sing.

*R. palumbina* Quél. [*R. grisea* (Pers. ex Secr. ut Agaricus) Fr. sensu Gillet, non (Pers. ex Secr.) Fr. sensu Secr.; *R. furcata* sensu Melzer & Zvára]; *R. ionochlora* Romagnesi (*R. grisea* (Pers. ex Secr. sensu Schäffer); *R. ornaticeps* Burl.; *R. parazurea* J. Schäffer; *R. sublevipora* (Romagnesi) Romagnesi; *R. ferreri* Sing.; *R. maxima* Burl.; *R. anatina* Romagnesi (*R. palumbina* Quél. sensu Melzer & Zvára unless conspecific with *R. ferreri*); *R. medullata* Romagn.; *R. stenotricha* Romagn.; *R. basifurcata* Peck; *R. spec.* (*R. medullata* Romagn. sensu Kühn.); *R. aeruginea* Lindbl. apud Fr. (*R. graminicolor* Quél. vix Agaricus graminicolor Secr.); certainly *R. subcompacta* Britz. sensu Sing. (but some of my specimens may be identical with *R. medullata* Romagn., others with *R. stenotricha* Romagn.); according to Bills also *R. redolens* Burl.

Note: I agree with Romagnesi (1967) that the species here enumerated should enter a single taxon. The fact remains that some species appear to be close to the following

\*The occurrence of these pigments, although more erratically, in other subsections of the *Rigidae* (*R. leucospora*, *R. cyanoxantha*, *R. virescens*), tends to confirm the affinity of the subsections here enumerated, especially those reunited in the section *Heterophyliae* in the sense of Romagnesi.

section; thus pallescent forms of *R. aeruginea* are sometimes extremely close to such representatives of sect. *Russula* as *R. pulchella*.

Subsect. *Amoeninae* Sing. Pileus brightly colored (pink, bright pink-red to red, purple to violet, green, lilac to almost black in the center, olive to partly brown, frequently bright yellow to dull yellow); stipe also either white or pink or purple or greenish or yellow; cuticle of the pileus and sometimes also the stipe with a characteristic bloom in dry weather; spore print A (then the taste not mild, either with a bitter component, or dermatopseudocystidia on pileus numerous), or B, C, or D; epicutis of the pileus consisting mainly of long hairs (piliform dermatocystidia) which also occur on the edge of the lamellae, or with a mixture of broadened subvesiculose terminal bodies and hair-shaped dermatocystidia, or with a mixture of ciliate dermatocystidia, primordial hyphae, and normal (often incrusted) hyphae (then pileus yellow, and taste not mild), or else with chains of broad elements forming a lower layer of the epicutis or a subcutis and a short ciliate dermatocystidium as terminal member (a structure intermediate between that of the *Lividinae* and the *Virescentinae*), and then with dermatopseudocystidia present but these gloeocystidial; a gelatinous subcutis absent or, if present, shallower than the epicutis and the hypodermium and often only subgelatinous; hypodermium of strongly interwoven hyphae passing into the trama of the pileus, taste mild, or slightly acrid in young lamellae, or more or less acrid and bitter at the same time.

Type species: *R. amoena* Quél.

Stirps *A m o e n a*. (Dermatopseudocystidia absent; cheilocystidia usually "empty" and acute; spore ornamentation most frequently ridged, rarely reticulate; pileus and stipe sometimes yellow; spore print never pure white, sometimes reaching D, at least B).

*R. mariae* Peck (*R. bella* Hongo; *R. aciculocystis* Bills & Miller\*); *R. alachuana* Murr.; *R. amoena* Quél.; *R. tuberculata* Murr.; *R. variicolor* Murr.; *R. violeipes* Quél.; *R. flava* Frost & Peck apud Peck; *R. variegata* Sing.

Stirps *Ochroleucoides*. (Pseudocystidia of the gloeocystidial type present; spore print Ia to IIa (Romagnesi-chart); pileus and often stipe yellow.)

*R. ochroleucoides* Kauffm. (*R. dura* Burl.).

Subsect. *Virescentinae* Sing. (1932). Pileus with a more or less continuous covering (epicutis) that is similar and perhaps partly homologous with the velar layer of the *Fistulosinae*, soon breaking into areolate patches and furfuraceous particles, consisting of spherocysts most of which are mucronate as a piliform or ciliate dermatocystidium arises from its upper side, with or without a septum (this structure, the

\*The "holotype" of *R. mariae* Peck indicated by these authors has either changed color (as frequently happens on drying in this subsection) or cannot be recognized as type as it does not correspond with the original color description of that species. But if *R. mariae* were really conspecific with *R. alachuana* Murr., the pinkish red species would have to be renamed *R. bella* Hongo, type and fresh authentic material seen (Herb. Hongo; F).

*Virescens*-structure, is characteristic for this one subsection of sect. *Rigidae*, for sect. *Pelliculariae* subsect. *Guayarenses*, and for the section *Plinthogali* of *Lactarius*).

Type species: *R. virescens* (Schaeff. ex Zanted.) Fr.

*R. chlorinosma* Burl. (*R. maculosa* Murr.); *R. patouillardii* Sing.; *R. virescens* (Schaeff. ex Krombh.) Fr.; *R. crustosa* Peck; *R. heterosporoides* Murr.; *R. alboareolata* Hongo; *R. epichnoa* Sing. ined.

Subsect. *Lilaceinae* Melz. & Zvára (1927). Pileus subglabrous, subvelutinous, or pruinose, bright colored, mostly blue to purple, red to pink, white, without dermatopseudocystidia, usually with numerous primordial hyphae; margin of the pileus rounded-obtuse;  $\text{FeSO}_4$  reacting normally; sulfovanillin reacting normally with the dried context of the stipe; spore print A to C.

Type species: *R. lilacea* Quél.

1. Species with at least scattered blue granules in some epicuticular elements in sulfovanillin mounts:

*R. subtilis* Burl.; *R. peckii* Sing.; *R. perplexa* Burl.; *R. nothofaginea* Sing.; *R. maior* Sing.; *R. montivaga* Sing.; *R. sericeonitens* Kauffm.

2. Species without any blue reaction in SV mounts:

*R. lilacea* Quél. with var. *lilacea* and var. *retispora* Sing.; *R. glaucescentipes* Murr.; *R. australirosea* Murr.; *R. mallophora* Sing.; *R. zvarae* Melzer; *R. azurea* Bres.; *R. uncialis* Peck; *R. praetenuis* Murr.; *R. subminutula* Sing. (*R. lilacea* var. *emeticolor* J. Schäffer); *R. subinconstans* Murr. (*R. inconstans* Murr. non Burl.); *R. pulchra* Burl.; *R. roseitincta* Murr.; *R. cremea* (Murr.) Sing. (*R. heterospora* var. *cremea* Murr.); *R. westii* Murr.; *R. lactea* (Pers. ex Fr.) Fr. [*R. heterophylla* (Fr.) Fr. p.p.]; *R. eogranulata* (Secr.) Sing.\*

Subsect. *Roseinae* Sing. Differing from the preceding subsection in strong positive reaction with sulfovanillin (bright red in dried stipe: "folly" Maerz & Paul).

Type species: *R. rosea* Quél.

*R. rosea* Quél. (sensu Sing. 1926) (*R. aurora* Krombh. sensu Melzer & Zvára, 1932); *R. minutula* (Velen.) Sing. with var. *robusta* Saini, Atri. & Sing.; *R. albida* Peck; *R. praeumbonata* Burl.\*\*

Subsect. *Lepidinae* Melzer & Zvára (1927). Pileus thick-fleshy, generally hard and firm, with subvelutinous to subtomentose cuticle which may contain non-macrocytidial pseudocystidia (which do not turn blue in sulfovanillin) and primordial hyphae; taste often bitter; margin firm and rounded-obtuse;  $\text{FeSO}_4$  and sulfovanillin reacting normally with the context; pseudocystidia of the lamellae not bluing with sulfovanillin (only becoming grayish hyaline); spore print A-B, more rarely C-D.

\*c.n. (*Agaricus eogranulatus* Secr., *Mycogr. Suisse* 1: 505. 1833).

\*\*Material from Michigan not compared with the type showed the SV reaction characteristic for this subsection. The anatomical data taken from the type point at either this or the preceding subsection.

*Type species: R. lepida* Fr.

*R. rosacea* (Pers. ex) Gray (*R. lepida* Fr.); *R. lepidiformis* Murr.; *R. luteobasis* Peck; perhaps also *R. hixsonii* Murr.

Subsect. *Xerampelinae* Sing. (1932) [*Luteogratae* subsect. *Viridantes* Melz. & Zvára ex Konr. & Joss. 1935; group *Viridantes* (without definite rank) Melzer & Zvára 1927]. Pileus whitish, brown or bright colored, with often rounded-obtuse margin, subglabrous to subvelutinous, with or without dermatopseudocystidia; lamellae not polydymous and not regularly forked; taste mild, or bitter, or very slightly acrid in the young lamellae; odor often of trimethylamin; context most frequently distinctly staining yellow or brown, or becoming so when old or on drying; spore print from A to almost G, most frequently B, C, D, or E;  $\text{FeSO}_4$  with context blue-green to olive green or gray-green, rarely brown (often in *R. fucosa*); spores often with very strongly echinate ornamentation (IV, VI).

*Type species: R. xerampelina* (Schaeff. ex Secr.) Fr.

*R. xerampelina* (Schaeff. ex Secr.) Fr. with numerous "varieties"\*\* in Europe, Asia, and America; *R. pseudolepida* Sing.; *R. oreina* Sing. (*R. favrei* Moser).

Subsect. *Pusillinae* Sing. Pileus rather thin and fragile; pileus bright red or rose color with transitions to yellowish ocher in one species, often pale colored in these colors; dermatopseudocystidia present; spore print from B-C to D;  $\text{FeSO}_4$  and sulfovillin reacting normally with the context, pseudocystidia bluing in sulfovillin.

*Type species: R. pusilla* Peck.

*R. humidicola* Burl.; *R. pusilla* Peck; *R. incarnatipes* Murr.; *R. cystidiosa* Murr.; *R. lividirosea* Murr.

*Note:* Some species are said to have acrid taste, but the anatomical analysis shows that there are no dermatopseudocystidia. This is against the rule valid for at least the sect. *Russula*, where all species with distinctly acrid taste also have dermatopseudocystidia (bluing in sulfovillin). The author has not studied the African species involved but the only American species coming into this category, *R. corallina* Burl., seems to belong to the *Rigidae* where it may be the type of a special subsection. *R.*

\*\*These "varieties" are quite constant. They may be considered as subspecies (in the sense of mycoecotype) or as species, forming a stirps *Xerampelina*. The type variety is var. *quercetorum* Sing.; other European species, subspecies, or varieties are *R. barlae* Quél. sensu W.G. Smith; *R. graveolens* Romell; var. *olivascens* (Fr. p.p.) Zvára]; *R. xerampelina* var. *pseudomelliolens* Sing. (*R. melliolens* sensu Crawshay); var. *marthae* Sing.; var. *elaeodes* Bres. (near the following variety); var. *rubra* (Britz.) Sing. (*R. Linnaei* Fr. sensu Ricken). The latter two varieties represent the European conifer races. In America, the forms corresponding to the type are either brighter red (*R. semirubra* Sing.), or with deeper (E) spore color (*R. squalida* Peck); a pale (C)-spored form (*R. fucosa* Burl.) is not very rare in New England, and a bright purple form in oak woods in New York may be determined as *R. subvelutina* Peck the type of which has been lost at Albany. *R. Arnoldae* Murr. is a typical Florida race. The Asiatic forms known to the author, are almost the same as those observed in Europe, but west of the Rocky Mts., in North America, and also in Florida, more species or subspecies or varieties belonging to stirps *Xerampelina* have been collected but have not been described except for some of them that were published (as independent species) by Murrill. *R. xerampelina* var. *pascua* Møller & J. Schäffer is the same as *R. oreina* Sing.

*heimii* Sing. (*R. velutipes* Heim non Vel.) and *R. citrinipes* Heim may also enter this group.

Sect. 10. *RUSSULA* [*Fragiles* Fr. 1938; *Firmae* Fr. 1838; *Alutaceae* R. Maire 1910; *Polychromae* R. Maire 1910]; *Constantes* Sing. 1926; *Acrirubentes* Konr. & Joss. 1935; *Carnosotenuis* Killermann 1936; *Coccineae* Romagn. 1962; *Leucosporae* Quél. 1888\*; *Xanthosporae* Quél. 1888\*\*]. Pileus glabrous and viscid when wet, and not pruinose, scurfy, sericeous, subvelutinous, subtomentose, areolate, etc. (except sometimes pruinose on the extreme margin or on the discolored disc with a detersive, fugacious pruina), unless the spores in print are deeper colored than D, or the context is very acrid and the lamellae are not regularly intermixed or forked; in one species, the pileus is sometimes subsericeous-floccose but then the reaction with FeSO<sub>4</sub> is normal and the flesh becomes yellow in age; FeSO<sub>4</sub> always reacting normally with the context, or else merely somewhat more toward the salmon orange side, or toward the pink side (by partial suppression of the grayish-sordid component) in some species, but reaction never negative or green; formalin negative; spore print from A to H; a distinct gelatinous subcutis and a distinct suprahilar amyloid spot on the spores present; sulfovanillin on dried stipe surface not persistently bright red; pigment not normally forming internal granules as in some *Rigidae*; epicutis never in form of a *Virescens*-structure nor epithelial. Most species temperate, some tropical-montane, very few tropical.

Type species: *R. emetica* (Schäff. ex Fr.) Pers. ex Fr.

I. Series of subsections with the spore print from B to C, and the taste acrid, or mild; context tending to stain yellow or brown; dermatopseudocystidia present or absent.

Subsect. *Melliolentiae* Sing. (1932); context with a tendency to become yellow or brown; spore print about B, more rarely reaching C; stipe rather stout and usually not longer than the diameter of the pileus.

Type species: *R. melliolens* Quél.

\*If *R. emetica* is accepted as the type species of this section, and the section itself is considered as such rather than as a combination of sections under a heading without definite rank, then, and only then, the *Leucosporae* become a synonym of sect. *Russula*. If the *Constantes* are excluded from the *Leucosporae* as they were by Lange's (1926) emendation, the selection of *R. emetica* becomes logical. However, the author tends to the opinion that both the *Leucosporae* and the *Xanthosporae* of Quélét are not actually intended to be sections but rather "headings" for the next-following divisions which are here considered as sections. Consequently, the sect. *Piperinae* Quél. 1888 also becomes a synonym of sect. *Russula*; sect. *Ingratae* has been taken up by R. Maire for the sect. 8 of this survey; sect. *Sapidae* would be another synonym of sect. *Rigidae* Fr.

\*\**R. lutea* is assumed to be the lectotype of this group. The author doubts, however, whether it is correct to consider the *Xanthosporae* as a section, and tends to the opinion that they are merely a common heading for what is actually meant to be the sections, i.e. the *Tenellae*, *Insidiosae*, and *Versicolores* Quél. 1888. If this view is accepted - and it would be desirable to accept it not merely as being in accord with the spirit of Quélét's treatment but also in order to avoid the introduction of thus far neglected subsectional names -, the *Tenellae* would be typified, according to the proposal of the author, with *R. lutea* as the lectotype, and would become another synonym of sect. *Russula*, the *Insidiosae* should be considered based on *R. maculata* Quél., and thus become another synonym of sect. *Russula*, and the *Versicolores* should be based on *R. olivacea* whereby they would also become synonymous with sect. *Russula*.

*R. brunneoviolacea* Crawshay (*R. pseudoviolacea* Joachim); *R. melliolens* Quél.; *R. viscida* Kudrna; perhaps also *R. purpurascens* Bres. (if different from the preceding forms) and *R. grossa* Berk.

Subsect. *Puellinae* Sing. (1932). Context with a tendency to become yellow-ocher; spore print about C (IIa-c, Romagnesi); stipe rather slender and fragile, usually longer than the diameter of the pileus.

Type species: *R. puellaris* Fr.

*R. puellaris* Fr.; *R. caucasica* (Sing.) Sing. (*R. puellaris* var. *caucasica* Sing.); *R. appalachiensis* Sing. (*R. puellaris* sensu Beardslee); *R. puellula* J. Schäffer & Möller; *R. microspora* Sing.

II. Series of subsections (*Fragiles* sensu Heim) with the spore print between A and E, taste acrid, rarely mild; dermatopseudocystidia very numerous.

Subsect. *Citrinae* Romagnesi (1962). Differing from subsection *Felleinae* (sect. *Ingratae*) by the absence of intraparietal pigmentation; pileus golden yellow, lemon yellow, greenish yellow, even with extensive colorless (white) zones.

Type species: *R. citrina* Gillet.

*R. citrina* Gillet; *R. raoultii* (Quél.) Sing.; *R. innocua* (Sing.) Sing.; *R. anomala* (Peck) (*R. subalbidula* Murr.); *R. solaris* Ferdinand & Winge.

Subsect. *Russula* (Emeticinae Melzer & Zvára (1927); *Acrirubentes* subsc. *Emeticae* Konr. & Jos.). Spore print A or B, rarely reaching C (scarcely in fresh spore prints), usually A or A-B, and if darker, spores with ornamentation VII, or at least fungi not corresponding to the diagnosis of the subsequent subsections.

Type species: *R. emetica* (Schaeff. ex Fr.) Pers. ex Fr.

Stirps *Atropurpurea*. [Ornamentation of the spores often very short (type VII), spore print A to B (C); pigment of the cuticle of the pileus in globules according to R. Maire, usually dark purple, rarely yellow-green.]

*R. bresadolae* Schulz. (*R. atropurpurea* (Krombh.) Britz. non Peck); *R. vinacea* Burl.; *R. norvegica* Reid (if different from *R. nigrodisca*); *R. aquosa* Leclaire, *R. fragilis* (Pers. ex Fr.) Fr. (with several forms); *R. citrinochlora* Sing. - *Alnus-mycorrhiza*: *R. alnijorullensis* (Sing.) Sing.\*; *R. pumila* Rouzeau & Massart; *R. alnetorum* Romagn.

This stirps is close to subsect. *Melliolentinae* (*R. melliolens* and *R. viscida*).

Stirps *Emetica*. (Ornamentation normally long, i.e. 0.4-1.5 µm; pigment red, not in globules; spore print A or A-B, - Romagnesi Ia-b - rarely reaching B.)

*R. emetica* (Schaeff. ex Fr.) Pers. ex S.F. Gray; *R. mairei* Sing.; *R. emeticella* (Sing.) Hora; *R. pantoleuca* Sing.; *R. perlactea* Murr.; *R. nigrodisca* Peck apud Macoun in Jordan (*R. fragilis* var. *alpestris* Boud.; *R. emetica* ssp. *alpina* Blytt; *R. nana* Killermann); *R. atrorubens* Quél. (sensu Lange, Romagnesi); obviously also

\*st. n. (*R. emetica* ssp. *alnijorullensis* Sing., Rev. Myc. 15: 133. 1950).

*R. betularum* Hora and *R. boyacensis* Sing.

Subsect. *Sardoninae* Sing. (1932). Spore print B-C, rarely C-E (Crawshay i.e. IIa to IIIc, Romagnesi chart); pileus usually purple, rarely partly red, rarely partly or entirely greenish or melleous; margin of the pileus acute or subacute or at first so, rarely becoming so; stipe usually pink or purple, rarely white; context of stipe negative or pink with NH<sub>4</sub>OH; ectomycorrhiza with conifers or *Betula*, not with Fagaceae.

Type species: *R. chrysodacryon* Sing.

*R. fallax* (Fr.) Britz. (sensu Pers. in herb.; Sing.); *R. queletii* Fr. apud Quél.; *R. torulosa* Bres.; *R. arenaria* Sing.; *R. chrysodacryoides* Sing.; *R. drimeia* Cooke; *R. chrysodacryon* Sing.; *R. pyrenaica* Blum ex Sing.; *R. subtorulosa* Sing.; *R. fusco-rubra* (Bres.) Sing.; *R. robinsoniae* Burl.; *R. gracilis* Burl. (*R. gracillima* J. Schäffer); probably also *R. altaica* Sing.\*

Note: A key to the species of this subsection has been published in *Collectanea Botanica* 13: 688-690. 1982.

Subsect. *Sanguineae* Melz. & Zvára (1927). Differs from the preceding subsection in a wider range of spore print color (Ia to IIIc) and ectomycorrhizal associations, and in more red, rose-red or carmine colors, and the context, if staining yellow, not pink with NH<sub>4</sub>OH; gelatinous subcutis often rather shallow as compared with epicutis and hypodermium; pileus in this case usually rather bright pinkish-blood red with poorly separable pellicle and context beneath tending to be pink (for tropical yellowing species compare also section 1, subsection *Heliochrominae*).

Type species: *R. sanguinea* Fr.

Stirps *Luteotacta*. (Strongly yellow staining; spore print Ia, Ib. Romagnesi).

*R. luteotacta* Rea.

Stirps *Sanguinea*. (Yellow staining or not; fresh spore print IIa to IIIa; typically sphagnicolous or else rarely or never ectomycorrhizal with *Betula* and *Picea*).

*R. mexicana* Burl.; *R. americana* Sing.; *R. martinica* Pegler in Pegler & Sing.; *R. rubicunda* Quél. (with several varieties or related microspecies); *R. sanguinea* Fr.; *R. helodes* Melzer.

Note: A key to the species of stirps *Sanguinea* has been published by Singer, Araujo & Ivory, *Beih. Nova Hedwigia* 77: 280. 1983.

Stirps *Pulchella*. (Not staining yellow; spore print IIIa-IIIc, Romagnesi, if not truly sphagnicolous, rather constantly forming ectomycorrhiza with *Picea*, otherwise with *Betula*).

*R. rhodopoda* Zvára; *R. pulchella* Borsczov (*R. palustris* Peck; *R. exalbicans*

\*Material described under this name (cf. Knudson & Borgen, *Arct. Alp. Myc.* p. 225. 1980) but with aeruginascent FeSO<sub>4</sub> reaction belongs in sect. *Rigidae* subsect. *Xerampeliniae*.

Melzer vix *Agaricus exalbicans* Secr.; *R. depallens* (Pers. ex) Fr. sensu J. Schäffer vix Fr.).

III. *Series of subsections* with the spore print from D to E (F), the taste mild or somewhat acrid in the young lamellae; context rarely tending to become yellow-melleous in the base; dermatopseudocystidia most frequently present, but often small and inconspicuous, rather rarely absent.

Subsect. *Betulinae* Romagnesi (1962)\* (Sphagnophilae Sing., Romagn. both nom. subnud.). Pileus bright red, purple red, purple brown, ochraceous tan, with dark center or (rather rarely) green; spore print IIa to IIIc; the entire carpophore or parts of it tend to become ocher or yellow in age only if spores deeper than IIId (Romagnesi), otherwise not yellowing; stipe usually either relatively small or considerably longer than the diameter of the pileus. Most species medium to small, fragile, ectomycorrhiza mostly with *Betula*.

Type species: *R. sphagnophila* Kauffman.

*R. disparilis* Burl.; *R. blackfordiae* Peck (*R. serotina* sensu Melzer & Zvára; *R. versicolor* J. Schäffer); *R. saliceticola* (Sing.) Kühn. ex Knudsen & Borgen (*R. sphagnophila* ssp. *saliceticola* Sing.); *R. sphagnophila* Kauffm. (*R. venosa* Vel. sensu Melzer apud J. Schäffer); *R. cristulispora* Sing. [*R. intensior* (Cooke?) Romagnesi]; *R. fontqueri* Sing.; *R. zonatula* J. Schäffer & Möller; *R. cernohorskýi* Sing. (1947) (*R. sphagnophila* var. *heterosperma* Sing.); *R. zelleri* Burl.; probably also *R. scotica* Pearson.

Subsect. *Integrae* R. Maire (1910). (*Integrinae* Sing. 1932; *Paludosinae* J. Schäffer, Romagn., nom. subnud.). Pigment of pileus often bright red, also more yellow, or even avellaneous, reddish brown, fulvous, bay, etc., but not livid or green and not multicolorous-pallid; stipe usually not stout but also not elongate, i.e. not longer than the diameter of the pileus in average, and not very fragile except in very old carpophores, white to reddish; pileus with dermatopseudocystidia, more rarely without them.

Type species: *R. paludosa* Britz. (= *R. integra* L. ex Fr. sensu Fr. p.p., see *Sydotia* 5: 457. 1951).

*R. integra* (L. ex Vitt.) Fr. (sensu Sing. (*R. velenovskyi* Melzer & Zvára); *R. fusconigra* Moser (*R. fuscomaculata* Romagnesi nom. subnud.; *R. fusca* Quél. sensu Sing.); *R. paludosa* Britz. (*R. elatior* Lindbl.; *R. rubrotincta* (Peck) Burl.); *R. luteensis* Romagnesi; *R. flaviceps* Peck (sensu Burl.); *R. beardsleei* Burl.; perhaps also *R. tricolor* Murr. (*R. patriotica* Murr.).

IV. *Series of subsections* (*Russulinae* in the sense of Singer 1926) with the spore print C-D to (E) F, F, F-G or H; taste mild, moderately acrid, strongly acrid, or bitter; context rarely tending to become yellowish, rather sometimes yellow from the start, or tending to become palest cinereous in the base; dermatopseudocystidia either present or absent. Species with bitter or acrid taste or odor of phenol or with

\*non Burl. 1915 (invalid, Art. 33.1, 35.4).

numerous primordial hyphae and no dermatopseudocystidia belong here even if the spore print is paler than G.

Subsect. *Olivaceinae* Sing. (1932). Spore print G or G-F or H; dermatocystidia none or not bluing in sulfovanillin; taste mild; phenol with context vinaceous-purple to deep lilac.

Type species: *R. olivacea* (Schaeff. ex Secr.) Fr.

*R. olivacea* (Schaeff. ex Secr.) Fr.; *R. alutacea* (Pers. ex Schwein.) Fr. sensu Melzer & Zvára; *R. vinosobrunnea* (Bres.) Romagnesi (*R. alutacea* spp. *eualutacea* f. *vino-sobrunnea* (Bres.) Sing.).

Subsect. *Amethystinae* Romagnesi (1963). Macrocytida blue on the tip only in sulfovanillin; phenol with context chocolate; odor usually of iodoform or phenol in the base of the stipe; pileus with a pruinose bloom; stature small to medium; mycorrhiza with conifers; spore print IIc to IVa; primordial hyphae numerous and dermatopseudocystidia absent on pileus and stipe surface.

Type species: *R. amethystina* Quél.

*R. murrillii* Burl.; *R. dadmunii* Sing.; *R. punctata* Krombh. (sensu Sing. = *R. turci* Bres. sensu Maire); obviously also *R. amethystina* Quél.

Subsect. *Chamaeleontinae* Sing. (1932). Context with phenol to chocolate (even though at times reaching a venetian red slowly deepening to chocolate); odor of iodoform absent; spore print deep ochraceous (IIIC to IVd) dermatopseudocystidia on the surface of the pileus either completely absent, or scattered and rare; taste mild; mycorrhiza with conifers or other trees.

Type species: *R. chamaeleontina* Fr.

*R. chamaeleontina* Fr. sensu Romagn. (*R. armeniaca* Cooke; *R. lutea* f. *luteorosella* Britz.); *R. lutea* (Huds. ex Fr.) S.F. Gray with var. *montana* Sing. and var. *ochracea* (Pers. ex Fr.) Sing.); *R. roseipes* Secr. ex Bres.; *R. neglecta* Sing. (*R. turci* Bres. p.p.; *R. multicolor* Blum nom. nud.; *R. chamaeleontina* Fr. sensu Schäffer 1939, 1952); *R. postiana* Romell (*R. mollis* Quél. sensu Romagnesi); *R. subalutacea* Burl.; *R. amygdaloïdes* Kauffm.; *R. cremeoavellanea* Sing..

Subsect. *Laetinae* Romagnesi (1962). Dermatocystidia with acidoresistant granulation incrusted; context becoming chocolate with phenol; spore print IVb-c (Romagnesi-chart); taste often styptic, subacrid, or bitter; cuticle bright red; gelatinous subcutis shallow; mycorrhiza with frondose trees.

Type species: *R. borealis* Kauffm. sensu Sing.

*R. pseudointegra* Arn. & Goris; *R. borealis* Kauffm. (sensu Sing., Romagnesi; *R. melzeri* Zvára sensu Sing.).

Subsect. *Integroideae* (Romagn.) Romagn. (1962) s. str. Pileus shiny, deep purple, more rarely pale pinkish red; surface of the pileus with bitter taste in most specimens; the pileus often umbonate; dermatopseudocystidia none or very scarce; spore print about F or F-G (Romagnesi ± IVb); primordial hyphae present; mycorrhiza with conifers.

*Type species: R. caerulea* ss. Cooke = *R. amoena* Britz.

*R. amoena* Britz. (*R. caerulea* sensu Cooke et al. non Pers., Fr.) with var. *austria-ca* Sing.

Subsect. *Firmiores* Konr. & Maubl. (1934) sensu str. Pileus mostly not remarkably shiny in dry condition, variously colored; not bitter even in the cuticle, not or exceptionally umbonate; dermatocystidia none or scarce and then not or very weakly reacting with sulfovanillin; spore print IIIc to IVd (Romagnesi-chart); spores usually with ornamentation type III, II. Mycorrhiza with Fagales, rarely conifers.

*Type species: R. aurata* (With. ex) Fr.

*R. aurata* (With. ex) Fr.; *R. grisea* (Pers. ex Secr.) Fr. (sensu Pers., Secr.! non Gillet, J. Schäffer, Romagnesi; *R. romellii* Maire sensu Romagnesi); *R. rubroalba* (Sing.) Romagnesi.

Subsect. *Polychromae* (Maire) Sing.\* Spore print G or H; cystidia strongly bluing in sulfovanillin and dermatocystidia numerous on the cuticle of the pileus; taste mild.

*Type species: R. polychroma* Sing. ex Hora (*R. integra* sensu Maire).

*R. polychroma* Sing. ex Hora (*R. integra* (L. ex Vitt) Fr. sensu Maire et al., non L. an Fr. p.p.?); *R. capensis* Pearson; *R. olivascens* Pers. ex (Schwein.) sensu Bres. non Romagnesi; *R. cessans* Pearson (*R. turci* Bres. p.p., sensu Sing. 1932); *R. tinctoria* (Secr.) Sing. comb. ined. (*R. chamaeleon* Sing.); *R. laricina* Velen.; *R. gilva* Melzer, *R. betulina* Burl. sensu orig.; *R. alutacea* ssp. *ambigua* Sing., *R. subluteobasis* Murr.

Subsect. *Rubrinae* Melzer & Zvára (1927). Spore print E-G (IIIb, Romagnesi) rarely H; dermatocystidia with acid-resistant fine incrustations or external guttulation; pileus very bright red; dermatopseudocystidia numerous and large; pileus strikingly opaque, rapidly drying and often with a slight bloom or scurf, or subvelutinous.

*Type species: R. rubra* (sensu Krombh., Bres.).

*R. picearum* Sing. (*R. rubra* "Fr." sensu Bres.); *R. pungens* Beardslee (probably = *R. rubra* "Fr." sensu Romagnesi); *R. kaviniae* Melzer & Zvára; *R. handelii* Sing.

Subsect. *Urentes* Maire (1910) (*Urentinae* Sing. 1932). Spore print G or H (IVa-IVd, Romagnesi), rarely between E and G with a tinge of F (IIId, Romagnesi); taste acrid (often only slightly so, often extremely acrid); dermatopseudocystidia numerous; odor of iodoform absent. Pl. 39.

*Type species: R. urens* Romell apud Maire ex Sing.

*R. nauseosa* (Pers. ex Schwein.) Fr.; *R. admirabilis* Burl.; *R. allescheri* Sing. (*R. nauseosa* var. *atropurpurea* All.); *R. nitida* (Pers. ex Fr.) (sensu Melzer & Zvára, Sing., non Schäffer; (*R. firmula* Schäffer); *R. transiens* (Sing.) Romagn.; *R. atro-violacea* Burl.; *R. mesospora* Sing.; *R. lundellii* Sing. (*R. pulcherrima* Schäffer); *R. schiffneri* Sing.; *R. veternosa* Fr. (sensu J. Schäffer); *R. aurantiolutea* Kauffm.; *R.*

\*stat. nov. (sect. *Polychromae* Maire, *Bull. Soc. Myc. Fr.* 26: 73. 1910).

*maculata* Quél.; *R. decipiens* (Sing.) Blum; *R. bresadoliana* Sing. (*R. veterosa* Fr. sensu Bres. non al.); *R. luteoviridans* Martin sensu Romagnesi; *R. pseudometatica* (Secr.) Sing. (sensu Sing. non Killermann; *A. pseudometricus* Secr. Var. B, 1833); *R. vinoso-purpurea* J. Schäffer (if different from the preceding); *R. macropoda* Sing.; *R. diaboli* Sing.; *R. badia* Quél.; *R. tenuiceps* Kauffm.; *R. piceetorum* Sing. (*R. adulterina* "Fr." sensu Romagnesi \*); *R. cinnamomicolor* Krombh.; *R. urens* Romell apud Maire ex Sing.; probably also *R. rutila* Romagnesi, according to Romagnesi's data also *R. subcristulata* Romagnesi, *R. cristulata* Romagnesi and *R. deceptiva* Romagnesi; also *R. cuprea* Krombh. sensu Romagnesi and *R. gigaspora* Romagnesi.

## 230. LACTARIUS (D.C. ex) S.F. Gray

*Nat. Arr. Brit. Pl.* 1: 623. 1821.

*Type species: L. torminosus* (Schaeff. ex Fr.) S.F. Gray\*\*.

*Syn.: Galorrhœus* (Fr.) Fr., *Syst. Orb. Veget.* p. 75, 1825; *Stirp. Agri Fems.* 3: 56. 1825, non Haworth (1812).

*Agaricus* trib. *Galorrhœus* Fr., *Syst. Mycol.* 1: 61. 1821.

*Lactifluus* Roussel ex O. Kuntze, *Rev. Gen. Pl.* 2: 856. 1891.

*Lactariella* Schröter in Cohn, *Krypt.-fl. Schlesien, Pilze* 3: 534. 1889.

*Lactaria* Pers. ex Schröter in Cohn, l.c. p. 534, non Rumph. ex Rafin. (1838).

*Lactariopsis* Henn., *Engl. Bot. Jahrb.* 30: 51. 1901.

*Hypophyllum* Paulet ex Earle, *Bull. N.Y. Bot. Gard.* 5: 408. 1909.

*Gloeocybe* Earle, l.c., p. 409.

*Characters:* Pileus and stipe usually fleshy, often vividly colored; cuticle varying in structure; hymenophore ordinarily lamellate; the lamellæ usually alternating with the lamellulae (lamellæ polydymous), moderately brittle, or not brittle at all, subdecurrent to decurrent, distant to crowded, thick to moderately thin, wedge shaped (Pl. 27, 1); basidia normal, 4-spored, rarely 2spored; true cystidia sometimes present and then often thick-walled (Pl. 27, 1); cheilocystidia sometimes present; macrocystidia commonly present, more rarely absent; hymenophoral trama subregular to subirregular and intermixed with laticiferous hyphae (Pl. 27, 1) and in very few cases also with spherocysts; spore print white to deep ochraceous or pinkish cream; spores (Pl. 54) under the microscope as in *Russula* but ornamentalizations from I-III are more frequent than in *Russula*; stipe usually central, more rarely eccentric or lateral,

\* This species is so close to *R. polychroma* that it might be considered better placed in subsect. *Polychromae*. The same is true for *R. nauseosa* and *R. admirabilis*, if the taste of young lamellæ is considered negligible. The two subsections may be revised with regard to their delimitations against each other.

\*\*Some authors prefer *A. piperatus* L. as lectotype for the genus. This would be equally acceptable had not the authors who first proposed it overlooked the fact that Fries (*Epicrisis* p. 340) states that "Linnaei e Fl. Suec. descr. ab utroque alienus!" It cannot be accepted for the species as understood by Fries, or the authors quoted by him.

The earliest acceptable designation of a type species under Art. 8.1 is that of Singer (1936) and Imai (1936) which must be followed. *L. deliciosus* cannot be accepted as type species of *Lactarius* inasmuch as the reasons for rejecting *L. torminosus* have no basis in the rules (cf. *Mycologia* 72: 649. 1980). *Lactarius* is not a homonym of *Lactaria* nor an avowed nomen novum but a new status of De Candolle's section *Lactarius* (pre-1821).

veiled, or more often without a veil; pigments present all through the carpophore (not merely in the cuticle of the pileus), more rarely absent in the lamellae or the stipe, often membranal or intercellular and, in many species, at the same time also intracellular; context with latex (except for older, dry specimens), either forming droplets of latex which may be watery or milky, or merely moistened from the colored, milky latex; Wood's light and polarized light causing little luminescence in most species; laticiferous hyphae running through the tissue, very striking (Pl. 27, 1; 34). On the ground in woods, usually forming mycorrhiza, more rarely on decayed wood.

*Development of the carpophores:* Some species are "pseudoangiocarpous" (probably pileoangiocarpous); others are gymnocarpous (Reijnders 1963, 1976 - only three species studied in detail); others are mixangiocarpous (Watling).

*Area:* Practically cosmopolitan.

*Limits:* See *Russula*, p. 807. Other genera with latex are: *Lactocollybia*, *Mycena*, *Entoloma*, *Bertrandia*, *Bondarzewia*, and one form of *Termitomyces*.

*State of knowledge:* The genus *Lactarius* is comparatively well known.

Most of the species have not been studied as thoroughly from all points of view as those of *Russula*, but there are usually more macroscopical characters on which the species concept can be based than there are in *Russula*. The number of species admitted in the following survey is 122. I enumerate in the main treatment only the sections well known to me. For additional or overlapping sections used to classify the palaeotropical Lactarii by Heim, see p. 837-839. A recent monograph by Hesler & Smith (1979) will be helpful for the identification of most North American species.

*Practical importance:* Lactarii are used for food in many countries, especially *L. deliciosus* and *L. sanguifluus* in Europe and Asia, also in North Africa. Enormous quantities of these species are annually sold in the markets of Barcelona, and other Catalonian cities. *L. resimus* and *L. scrobiculatus* are highest prized in Russia, where they are mostly salted (like sauerkraut) or pickled to be consumed with sour cream and vodka. However, all other Lactarii, including *L. torminosus* and *L. pipерatus* are also used for the same purpose. *L. torminosus* is also used fresh. The only species that seem to be poisonous are *L. helvus* and *L. pallidus*, but it is doubtful whether only in cooked form, or also in pickled form. Muscarin and stereoisomeric alcaloids have also been found in *L. rufus* and *L. trivialis* (Stadelmann et al. 1976) but both are used as pickles in USSR. Edible species of a very different flavor are those Lactarii that are here united in the section Dulces. The only one occurring in Europe, *L. volemus*, is frequently sold in the markets. Lactaroviolin (Heilbronner & Smith, *Helv. Acta Chim.* 37: 2018-2039, 1954) might become important because of its antibiotic activity against *Mycobacterium tuberculosis*; it has been isolated from *L. deliciosus*.

Species of the genus *Lactarius* are a good source for various raw materials for drug production but since no practical means for cultivation of the fruiting bodies has been worked out, and the supply must be based on the carpophores gathered in the woods, it is unlikely that the Lactarii as such become industrially important.

As ectomycorrhizal fungi, the *Lactarii* may yet become important in forestry. Some species form mycorrhiza with conifers, others with frondose trees, mainly of the orders Salicales and Fagales, but also of leguminous trees (Caesalpinoideae), Sapotaceae, and Polygonaceae in the tropics. At least one species is a root parasite.

## SPECIES

Sect. 1. *PANUOIDEI* Sing. (1957). Pleurotoid. Some species partly dimitic, some parasitic.

*Type species:* *L. panuoides* Sing..

*L. panuoides* Sing.; *L. igapoensis* Sing.; *L. campinensis* Sing.; *L. uyedae* Sing.

Sect. 2. *LACTARIOPSIDEI* Sing. (1942). Pileus with a persistent pilose-tomentose covering which consists of thick-walled hairs; stipe frequently annulate or otherwise veiled, more rarely developing gymnocarpously and then differing from most other *Lactarii* in having an almost or quite heteromerous hymenophoral trama; pseudo-cystidia (often gloeocystidia) on the sides of the lamellae numerous and voluminous; spores with medium sized ornamentation (which does not correspond to the type I and to the type VI), ovoid-subellipsoid (neither globose nor suborthotropic); context brittle; lignicolous, or on humus rich in woody matter. Tropical species.

*Type species:* *L. zenkeri* (Henn.) Sing.

*L. zenkeri* (Henn.) Sing.; *L. pandani* Heim.; *L. gymnocarpus* Heim apud Sing.; *L. neotropicus* Sing.; *L. annulifer* Sing. in Sing. & Araujo.

Sect. 3. *POLYSPHAEROPHORI* Sing. (1972). Taste mild; pileus dry but not with barbate margin; latex in older specimens often sparse; epicutis consisting of dermatocystidia which are more or less thick-walled and palisadic and rise from the sphaerocystoid cells of the hypodermium or between them; spores heterotropic; spore print pallid or slightly cream; sphaerocysts in the hymenophoral trama numerous, even near the edges of the lamellae. Tropical species.

*Type species:* *L. veraecrucis* Sing.

Subsect. *Polysphaerophorini* Sing. (1972). Latex white.

*Type species:* *L. veraecrucis* Sing.

*L. veraecrucis* Sing.; *L. amazonensis* Sing. in Sing. & Araujo; *L. subpallidipes* Sing. in Sing. & Araujo; *L. pallidipes* Sing. in Sing. & Araujo; *L. mamorensis* Sing. in Sing. & Araujo; *L. venezuelanus* Dennis; *L. paulensis* Sing. in Sing. & Araujo; *L. brasiliensis* Sing. in Sing. & Araujo.

Subsect. *Rubroviolascentini* Sing. (1942) with almost transparent, pale reddish gray or white, blackening, reddening or browning latex.

*Type species:* *L. rubroviolascens* Heim.

*L. nebulosus* Pegler; *L. rubroviolascens* Heim; perhaps also *L. russula* Rick.

Sect. 4. *VENOLACTARIUS* (Heim 1938) Sing. Pileus with an uppermost covering layer consisting of an epicutis of thin-walled elements forming an epithelium or hymeniform layer; hymenophoral trama filamentous; pseudocystidia present on the sides of the lamellae; spores nearly globose and subsymmetric-suborthotropic, with a very high ornamentation of type I or II or III; context rather tough; lignicolous, or on humus rich in woody matter. Tropical species.

Type species: *L. adhaerens* Heim.

*L. adhaerens* Heim; *L. reticulatus* (Berk.) Sing. (Panus, Berk.); *L. subreticulatus* Sing. in Sing. & Araujo.

Sect. 5. *DULCES* Heim (nom. subnud. ad. int.) ex Sing. (1942) (*Rhysocybe* Neuhoff 1956, p.p.). Taste completely mild except in one Brazilian species; pileus completely dry; latex extremely and strikingly abundant, unchanging or changing on exposure; cystidia either absent or present, and then not similar to the common pseudocystidia; sphaerocysts present only in the upper fifth of the lamellae (near the trama of the pileus, edge-near four fifths mostly quite free of spherocysts); spores either heterotropic or suborthotropic; cuticle often with an epicutis consisting of a palisade of dermatocystidia (not dermatopseudocystidia) and never with "Viresent structure"; spore print white or pale cream (A to B, Crawshay).

Type species: *L. volemus* (Fr.) Fr.

Subsect. *Fulgentes* Heim (1938). Spores suborthotropic.

*L. fulgens* Heim.

Subsect. *Lactifluini* (Burl. as "group" subdividing sect. *Russularia*) Sing. (1942). Latex staining brown or unchanging but always initially white or serifluous-white, not watery-transparent; spores heterotropic; thick-walled cystidia present or absent. Pl. 27, 1.

Type species: *L. volemus* (Fr.) Fr.

*L. pseudovolemus* Heim; *L. hygrophoroides* Berk. & Curt. (*L. distans* Peck); *L. braunii* Rick (if not too close to the preceding species); *L. volemus* (Fr.) Fr.; *L. allochrous* Sing.; *L. purgatori* Sing. (*L. austrovolemus* Hongo); *L. luteolus* Peck (*L. kuehnerianus* Malençon); obviously *L. caribaeus* Pegler; *L. putidus* Pegler; perhaps *L. clarkei* Cleland.

Sect. 5. *PLINTHOGALI* (Burl. ut "group" in *Russulariis*) Sing. (1942). Cuticle with distinct Viresent structure (Pl. 34), velutinous to subglabrous-subvelutinous, variously colored, often white, or gray, or avellaneous-umber, or deep warm sepia to almost black; dry; latex milky white, or colored, or watery, and then colored, often white and then reddening, but also persistently white, or staining deep violet. Spores, at least in the European species, ocher (E-F, Crawshay) in print; crested-reticulate (type I or II).

Type species: *L. lignyotus* (Fr. to Fr.) Fr.

Subsect. *Fuliginosi* (Konr. 1935 ut "groupe" subsectionis *Coloratorum*) Sing. (subsect. *Nigroviolascens* (Smith & Hesler) Bon.). Latex milky, not yellow.

Type species: *L. fuliginosus* (Fr. ex Fr.) Fr.

*L. gerardii* Peck; *L. pterosporus* Romagnesi; *L. lignyotus* Fr.; *L. nigroviolascens* Atk.; *L. fuliginosus* (Fr. ex Fr.) Fr. (with three subspecies); *L. costaricensis* Sing. in Sing. & Araujo; *L. sublatus* (Murr.) Sing. (Melanoleuca, Murr.); *L. gigasporus* Sing. in Sing. & Araujo and apparently also some African species\* and *L. brunneoviolascens* Bon as well as numerous North American species described by Hesler & Smith.

Subsect. *Xanthhydrorheini* Sing. Latex watery, yellow.

*L. xanthhydrorheus* Sing.

Note: We have not studied the species described by Heim which seem to be referable to his new sect. *Pelliculares* (1959) with the type *L. pelicularis* Heim from tropical Africa. This seems to be a good section but still vaguely limited (we refer to Heim's respective papers which shall be summarized in a supplementary note on tropical African *Lactarii*, p. 837-839).

Sect. 6. *ALBATI* (Bat.) Sing. 1942 (*Velutini* subsect. *Albati* Bat. 1908). Pileus dry, practically pigmentless; latex white or whitish, unchanging or more often somewhat changing on exposure, acrid (or at least context acrid); spores heterotropic; cuticle not showing any trace of Virescens-structure.

Type species: *L. vellereus* (Fr.) Fr.

*L. piperatus* (L. ex Fr.) S.F. Gray and related species\*\*; *L. subvellereus* Peck; *L. deceptivus* Peck; *L. vellereus* (Fr.) Fr.

Sect. 7. *RUSSULARES* (Fr. 1821 ut sect. *Galorrhæi*) Fr. 1838 (ut tribus\*\*\*). (*Prui-nati* Quél. 1888, max. e parte). Pileus dry, or slightly viscid, often subpruiniate, or slightly tomentose-subsquamulose, azonate or rarely zonate (and then mostly rufous-buff to dark cinnamon); lamellae becoming rather deep colored and consequently the spore dust distinctly visible as a paler powder on darker background; taste mild, bitter, or acrid; odor sometimes cumarinous; latex never colored from the beginning, never changing by exposure to anything but a light yellow (or else light cream from the beginning), sometimes watery or serifluous, but more often

\*One of which I have studied (FH); others seem to be: *L. melanodermus* Heim; *L. craterelloides* Heim & Goossens; *L. pseudolignyotus* Heim; *L. melanogalus* Heim, but all these said to have white or whitish spore print like *L. gigasporus*.

\*\* *L. piperatus* in the broader sense consists of a group of species closely related to each other (at least in the southeastern states of North America) which differ constantly in minor macroscopical and certain chemical characters. The whole problem has not yet been worked out satisfactorily but the necessary data on the European forms are available in Neuhoff (1956) who distinguished *L. glaucescens* Crossl. See also Romagnesi, *Bull. Soc. Myc. Fr.* 96: 73. 1980.

\*\*\*Art. 33.5 (Int. Code 1983) recognizes Fries' tribus as validly published for subdivisions of genera. In *Lactarius*, they are now accepted as sections which make *Tricholomatoidei*, *Limacini*, and *Piperati* sub-sections.

milky; margin of the pileus crenate or transparently striate, or smooth and entire; covering of the pileus not consisting of thick-walled hairs; spores strongly heterotrophic; cuticle never with Virescens-structure; latex not extremely abundant, in the contrary, often rather scarce except in very young and fresh specimens; pigment never completely absent.

*Type species: L. subdulcis* (Bull. ex Fr.) Gray.

Subsect. *Colorati* Bat. (1908) (Griseini Sing. 1942). Pileus tomentose-squamulose and dry, not rufous-buff to deep cinnamon; taste mild to acrid; odor often sweetish, not of cumarin; pileus not transparently striate.

*Type species: L. glycosmus* (Fr. ex Fr.) Fr.

A. Species with milky latex:

*L. griseus* Peck; *L. glycosmus* (Fr. ex Fr.) Fr. sensu Lundell & Nannfeldt; *L. hibbardiae* (Burl.) Sacc. [*L. glycosmus* Fr. sensu Neuhoff 1937; *L. confusus* Lundell apud Lundell & Nannf.\*]; *L. lilacinus* (Lasch) Fr. (with three subspecies, see *Ann. Mycol.* 40: 125, 1942); *L. pusillus* Bres. (*L. subalpinus* Kühner).

B. Species with watery latex. Odor cumarinous:

*L. helvus* (Fr.) Fr.

Subsect. *Olentini* Sing. (1942) (*Olentes* Bat., a subdivision of subsect. *Fucati*, sect. *Pruinati*). Cheilocystidia conspicuous; pseudocystidia on the sides of the lamellae usually absent or very scarce; odor of the dried, and sometimes of the fresh carpophores strongly cumarinous; latex often watery, or serifluous, but also sometimes milky, unchanging.

*Type species: L. camphoratus* (Bull. ex Fr.) Fr.

*L. camphoratus* (Bull. ex Fr.) Fr. with var. *fragilis* Burl. (*Agaricus rutaceus* Lasch); *L. serifluus* (D.C. ex Fr.) Fr.

Subsect. *Rufini* Sing. (1942). Pileus glabrous to subtomentose or thinly tomentose; latex milky, white, unchanging, acrid; pileus zonate or azonate; rufous to deep rufous cinnamon.

*Type species: L. rufus* (Scop. ex Fr.) Fr.

*L. rufus* (Scop. ex Fr.) Fr.; *L. peckii* (Burl.) Sacc. (*Lactaria*, Burl.; *Lactaria praezonata* Murr.); *L. alachuanus* Murr.

Subsect. *Obscuratini* Sing. (*Striatini* Sing. ex Heim ut *Striati*, subsectio *Pruinosorum*, typo excluso). Pileus transparently striate. Epicutis containing cellular elements which appear clearly on a scalp preparation of the cuticle.

\*This species is called *L. mammosus* (Fr.) Fr. by Neuhoff (1956), and *L. subumbonatus* Lindgr. (1845) and *L. fuscus* Roll. (1899) are names as synonyms. The European specialists will have to decide on these matters in the end; in the meantime an unmistakable binomial backed up by a type specimen is still preferred here: *L. hibbardiae*.

Type species: *L. obscuratus* (Lasch) Fr.

*L. obscuratus* (Lasch) Fr. [*L. obnubilus* (Lasch) Fr.]; *L. tabidus* Fr.; *L. alni* Sing.; *L. guanacastensis* Sing. in Sing. & Araujo; *L. caucae* Sing.

Subsect. *Subdulcini* Sing. (1942) (*Subdulces* Bat. 1908, a subdivision of subsect. *Dulces* of sect. *Pruinati*). Pileus not squamulose or rimose, not subtomentose to tomentose, but always subglabrous to subpruinate, dry, or slightly viscid, azonate, or somewhat zonate, rufous-buff to deep cinnamon; pseudocystidia usually numerous on the sides and edges of the lamellae; odor not cumarinous; margin not transparently striate; latex milky to somewhat serifluous, white, or more rarely cream color, and often turning cream color or sulphureous when exposed; taste mild, bitter, or acrid.

Type species: *L. subdulcis* (Pers. ex Fr.) Gray \*.

*L. subdulcis* (Pers. ex Fr.) S.F. Gray; *L. rugosus* Velen. (sensu Z. Schaefer); *L. hradecensis* Z. Schaefer; *L. fulvissimus* Kühn. & Romagnesi; *L. mitissimus* Fr. sensu Kühn. & Romagnesi; *L. quietus* Fr.; *L. hepaticus* Plowright apud Boudier; *L. decipiens* Quél.; *L. castaneobadius* Pegler; *L. murinipes* Pegler; *L. ferrugineus* Pegler; *L. quercuum* Sing.; *L. badiosanguineus* Kühn. & Romagnesi and many other North-temperate species.

Sect. 8. *LACTARIUS* (*Piperites* Fr. 1838 ut tribus). Pileus more or less viscid to glutinous, rarely dry and then neither velutinous nor pruinate and not completely pigment-less; latex milky, white at first, and remaining so, or changing color (to yellow purple, lilac, violet, olive, gray) by shorter or longer exposure to the oxygen of the air; lamellae rather pale-colored, and not strikingly powdery from the light colored spore masses in age; taste subacid to extremely acrid; pigment rarely a deep rufous buff to deep cinnamon, and odor of dried specimens never strongly cumarinous; margin of the pileus never transparently striate; covering of the pileus not consisting of thick-walled hairs; spores strongly heterotrophic; cuticle never of the Virescens-structure; latex not extremely abundant but fairly abundant in adult specimens under normal growth conditions; pigment rarely completely absent.

Type species: *L. torminosus* (Schaeff. ex Fr.) Gray.

Subsect. *Pyrogalini* Sing. (1942). Latex unchanging; pileus dull colored, often not viscid.

Type species: *L. pyrogalus* (Bull. ex Fr.) Fr.

*L. pyrogalus* (Bull. ex Fr.) Fr. and its various subspecies (see *Ann. Mycol.* 40: 123. 1942); perhaps also *L. circellatus* Fr.

Subsect. *Lactarius* (*Tricholomatoidei* Fr.; *Limacinia* Fr.; *Insulsini* Sing. (1942)). Pileus and latex as in the preceding subsection but pigments brighter: yellow, flesh color, orange, red.

\* Z. Schäfer (1966) insists that *L. rugosus*, not *L. hradecensis* corresponds to *L. subdulcis* sensu Kühner & Romagnesi non Pers. About the type of *L. subdulcis* (Pers. ex Fr.) S.F. Gray see Singer, *Persoonia* 2: 46. 1961.

Type species: *L. torminosus* (Schaeff. ex Fr.) S.F. Gray.

Note: This subsection is closely related to certain species of the *Russulares*, e.gr. *L. quietus* and some *Rufini*.

Stirps *Insulsus*. (Pileus slightly pubescent on the extreme margin, or more frequently wholly glabrous.)

*L. controversus* (Pers. ex Fr.) Fr. (*Agaricus albidorozeus* Gmelin); *L. cremeus* Z. Schäfer; *L. pallidus* (Pers. ex Fr.) Fr.; *L. zonarius* (Bull. ex St.-Am.) Fr. sensu Neuhoff; *L. insulsus* (Fr.) Fr.; *L. bresadolianus* Sing. (*L. zonarioides* Kühn. & Romagnesi); *L. acerrimus* Britz.; *L. roseozonatus* (v. Post ex Fr.) Britz.\* (*L. flexuosus* var. *roseozonatus* v. Post ex Fr.); *L. hysginus* (Fr. ex Fr.) Fr.; *L. porninsis* Rolland; *L. musteus* Fr.

Stirps *Torminosus*. (Margin barbate.)

*L. torminosus* (Schaeff. ex Fr.) Gray, spp. *torminosus* and ssp. *pubescens* (Fr.) Konr. & Favre; also obviously *L. mairei* Malençon.

Subsect. *Croceini* Sing. (1942) ("Group" *Croceae* Burl.). Latex changing to bright yellow after a short time of exposure.

Type species: *Lactaria crocea* Burl.

Stirps *Chrysorheus*. (Pileus slightly pubescent or glabrous on the margin.)

*L. chrysorheus* Fr. and its American satellites, such as *Lactaria crocea* Burl. etc. (perhaps not all of them worthy of specific distinction).

Note: This stirps is closely related to certain species of the *Russulares*, e.gr. *L. thejogalus*, and represents a continuation of the *Subdulcini* in the same manner as subsect. *Lactarius* is a continuation of certain groups in the *Russulares*.

Stirps *Scrobiculatus*. (Margin barbate.)

*L. resimus* Fr.; *L. citriolens* Pouzar; *L. scrobiculatus* (Scop. ex Fr.) Fr.

Subsect. *Aspideini* Sing. (1942) ("Groups" *Aspideae* and *Speciosae* Burl.). Latex becoming violet, slate-lilac, purple when exposed to the air, or the context staining in one of these colors when bruised.

*L. aspideus* (Fr. ex Fr.) Fr.; *L. aspideooides* (Burl.) Sacc. (perhaps not specifically different from the preceding species); *L. uvidus* (Fr. ex Fr.) Fr.; *L. luridus* (Pers. ex Fr.) Gray; *L. psammicola* A.H. Smith; *L. repraesentaneus* Britz.; *L. speciosus* (Burl.) Sacc. (perhaps not specifically different from the preceding species).

Subsect. *Vietini* Sing. (1942) (*Turpini* Neuhoff 1956) ("Groupe" *Vieti* Konrad of subsect. *Glabrati* Bat.). Latex or context turning gray, olive or sordid pale ochra-

\*Lange considers *L. flexuosus* (Pers. ex Fr.) S.F. Gray a doubtful species and calls his species - identical with the one so common in Southern Finland and studied there by the present author - as above (*L. roseozonatus*). Others take the opposite view and simply make *L. roseozonatus* a synonym of *L. flexuosus*. Since our observations coincide with those of J. Lange, we follow him, at least for the moment.

ceous on exposure (often only after considerable time); pileus and stipe often gray or green.

*Type species: L. vietus* (Fr.) Fr.

Stirps *Trivialis*. (Pileus subviscid to viscid, with glabrous margin; mycorrhiza with conifers and *Betula*.)

*L. vietus* (Fr.) Fr.; *L. trivialis* (Fr. ex Fr.) Fr.; probably also *L. akanensis* Imai; possibly also *L. umbrinus* (Pers. ex Schwein.) Fr. and (the true) *L. mammosus* Fr. (cf. Moser, *Kew Bull.* 31: 530. 1976; M. moseri Harmaja).

Stirps *Blennius*. (Pileus glabrous, strongly viscid; mycorrhiza with broad-leaved trees, ordinarily *Fagus*.)

*L. blennius* (Fr. ex Fr.) Fr. and its forms and varieties.

Stirps *Necator*. (Pileus villous at the margin, more less viscid.)

*L. necator* (Bull. em. Pers. ex Fr.) Karst. [Agaricus, Pers. ex Fr.; Lactaria, Schröter in Cohn non Agaricus necator Bull. (em. &) ex Gmelin 1825; Lactarius turpis (Weinm.) Fr. sensu Fr. et aut. non Weinm.; *L. necans* S.F. Gray; *L. plumbeus* (Bull. ex) Quél. non Fr. 1821]; *L. atroviridis* Peck.

Sect. 9. *DAPETES* Fr. (1828). Pileus more or less viscid, often zonate, often orange, violet, or blue; latex milky and opaque, sometimes not forming droplets but merely a fine moisture on bruised tissue, always colored from the beginning: orange, red, purple, violet, blue; cheilocystidia often well differentiated.

*Type species: L. deliciosus* (L. ex Fr.) S.F. Gray.

*L. deliciosus* (L. ex Fr.) S.F. Gray; *L. chelidonium* Peck; *L. pseudodeliciosus* Burl. (ut *Lactaria*); *L. salmoneus* Peck; *L. sanguifluus* (Paulet ex) Fr.; *L. subpurpureus* Peck; *L. paradoxus* Beardslee & Burl. (ut *Lactaria*); *L. indigo* (Schwein.) Fr.; obviously also a number of microspecies and related species recently separated and published by R. Heim and A.H. Smith and others.\*

*Supplementary note on the tropical African species of Lactarius:*

Heim [1938\*\*] and again 1955\*\*\* has published monographs on these species elabo-

\*What may be termed the stirps *Deliciosus* has recently been split up by some Japanese authors, later by Heim, Pouzar, Romagnesi, A.H. Smith and Hesler & Smith into at least three taxa (ranging from formae to species) but their descriptions are still somewhat overlapping. It is, however, probable that *L. deliciosus* has to be maintained in a restricted sense (Fries; Bresadola), and that we have to add *L. salmonicolor* Heim & Leclair in Heim = *L. subsalmoneus* Pouzar (*L. salmoneus* Heim & Leclair non Peck), *L. laeticolorus* (Imai) Imazeki, *L. deterimus* Gröger and *L. semisanguifluus* Heim & Leclair (but *L. akahatsu* Tanaka may be this latter, perhaps an earlier name!) in Europe, and probably more species in Japan and North America. Both *L. salmonicolor* and *L. semisanguifluus* have been seen fresh and dried, incl. authentic material, by the present author, but one cannot but agree with Kühner & Romagnesi who seem still somewhat sceptic as to whether these two species are actually tenable on the specific level or merely separable on the infraspecific level.

\*\**Les Lactaires-Russulés du domaine oriental de Madagascar*, Paris 1938 (publ. 1938).

\*\*\**Les Lactaires d'Afrique intertropicale*, *Bull. Jard. Bot. de l'État Bruxelles* 25(1): 1-91, 6 pls. March 1955, and *Lactarius* in W. Robyns, *Flore Iconographique des Champignons du Congo*, 4: 1-97, pl. xiii-xv. March 1955.

rating two successive classifications which, especially the later one, could not be co-ordinated with the system of classification adopted in the present work. Unfortunately, some important data on some of the species, such as would have to be taken up as type species of the proposed taxa, are missing, and Heim disposed of material not seen by the present author. For this reason we give his classification of the tropical African species in form of a short digest as an appendix to the classification accepted by us on the basis of material seen by us, in the hope that a later integration will be possible:

Sect. *CAPERATI* Heim (1955, nom. subnud.). Pileus at the same time grooved and marked with cerebriform veins which are generally concentric, and are also found on the apex of the stipe ... Basal mycelium abundant. Spores tuberculate or reticulate with low ornamentation, never crested.

“Groupe” *Lactariopsis* Here *L. pandani* Heim and *L. zenkeri* Henn. (with annulus or peripedicular pad).

“Groupe” *Gymnocarpi*. Here evelate forms with white latex: *L. gymnocarpus* Heim, *L. cinnamomeus* Goossens & Heim.

“Groupe” *Phlebonemi*: Here evelate forms with white, ochraceous or brownish latex, differing from the *Gymnocarpi* in closer, adnate rather than decurrent, thinner lamellae and thicker flesh: *L. caperatus* Heim & Goossens (apparently the logical type species of the section); *L. phlebonemus* Heim & Goossens.

Sect. *PTEROSPORI* Heim. This corresponds to our *Plinthogali* (see above) but the African species are here characterized by the white or little colored spores while the majority of the boreal species have ochraceous spore print; also, the main characters on which we base *Plinthogali*, the *Virescens*-structure of the cuticle, is not generally found in all species, so that Heim considers as basic character the deeply reticulated-winged spore ornamentation.

“Groupe” *Venolactarius*. Here the covering layers are said to be composed of large hairs with thick refringent walls, the pileus with gelatinous veins. *L. adhaerens* Heim and *L. nudus* Heim.

This group, according to Heim, may also be transferred to the *Caperati*.

Main group: *L. melanogalus* Heim; *L. melanodermus* Heim & Goossens; *L. cratelloides* Heim & Goossens; *L. nudus* Heim; *L. pseudolignyotus* Heim.

Sect. *COMPACTI* Heim (1955, nom. subnud.). Tall and thick species with pileus and stipe generally concolorous. Latex white or orange (this refers to *Dapetes*, group of *L. deliciosus*, not tropical-African). Vestiment of pileus [viscid\*], glabrous or very finely tomentose.

“Groupe” *Nigricantini*. Robust, compact species with pileus and stipe of the same color, dusky; vestiment of pileus “viscid or glabrous”, sometimes with striate

\*This refers to Barbatii and Immutabiles, temperate groups which Heim would include here, but also to some tropical species.

margin. Context reddening or browning. Spores verrucose. Here only *L. pellucidus* Goossens & Heim.

“Groupe” *Volemi*. Robust species with the margin of the pileus not striate. Pileus and stipe concolorous. Context or latex discolored on exposure to the air, latex at first white or transparent-gray. Surface of pileus dry, tomentose, velutinous, or pruinose, ochraceous brown or orange. This apparently combines the various subsections of our sect. *Dulces* (see above). Here, according to Heim: *L. rubro-violascens* Heim; *L. angustus* Heim & Goossens; *L. pseudovolemus* Heim, and of extra-African species: *L. clarkei* Cleland; *L. volemus* Fr.

“Groupe” *Ingrati*. Pileus glabrous, dusky colored, with striate-pectinate margin which is acute. Taste acrid and odor little agreeable. Context remaining white. Here only: *L. corbula* Heim & Goossens.

Sect. *GENUINI* Heim (1945, nom. subnud.). Species which are not tall but sometimes rather large, not combining the characters of the following and preceding sections. This, in the sense of Heim, combines most of the boreal species or sections; only one African group, *Floccosi*, which is meant to combine “part of the *Velutini* Quél. (among them, the majority of the *Colorati* Bat. have been put in the *Pterospori*), and also the *Floccosi* Kühner, or the majority of the *Constantes* of Konrad, with various tropical species”. In tropical Africa: *L. fulgens* Heim, and *L. velutinus* Bres. as well as 5 other species of the Congo.

Sect. *PELICULARES* Heim (1955, nom. subnud.). Pileus membranous, with deeply sulcate-canaliculate, eventually obtuse margin, brightly colored. Stipe eventually becoming hollow. Lamellae not very close. Latex dirty white, acrid. Here two species: *L. pellicularis* Heim (apparently a candidate for type species of the section); *L. chamaeleontinus* Heim.

Heim thinks that this group is analogous with the *Pelliculariae* of the genus *Russula*.

#### GENERA EXCLUDENDA ET INCERTAE SEDIS

In this category enter all those genera of Agaricales and genera confused with Agaricales in the past insofar as they do not enter any of the families here recognized, either because they are definitely fungi belonging to some other order, or because they are incompletely known and cannot be determined with any degree of probability as far as the order or family to which they belong is concerned. As far as these are still suspected to belong to the Agaricales, they are mostly genera based on type species whose type or authentic material has been lost.

All these genera are here enumerated, shortly characterized where necessary, and discussed where possible, in alphabetical order:

*Amylaria* Corner, *Bull. Brit. Mus.* 1: 197. 1955, a “clavariaceous” genus with *A. himalayensis* Corner as type species was introduced in the Bondarzewiaceae by some authors (Donk, *Persoonia* 3: 247. 1964). It is, however, so completely different macromorphologically, in hyphal structure, spore size and lack of laticiferous

hyphae that Corner's proposal (and Pegler & Young's confirmation, *Trans. Brit. Myc. Soc.* 58: 49-58. 1972) to separate it from *Bondarzewia* and the Bondarzewiaceae is fully justified. The Amylariaceae, however, may (or may not) turn out to be synonymous with the Auriscalpiaceae.

*Arcangeliella* Cavara, *Nuov. Giorn. Bot. Ital.* 7: 117. 1900, see p. 807.

*Boletium* Clements, *Gen. Fungi*, p. 108. 1909, see *Volvoboletus*.

*Boletopsis* Fayod, *Malpighia* 3: 72. 1889. This is based on *Polyporus melaleucus*, an obviously misspelled version of *Polyporus leucomelas* Pers. ex Fr. Donk, R. Maire, and Singer have recognized this genus, but it belongs in the Thelephorineae Herter where it is the only representative of a family Boletopsidaceae (Donk ut tribus) Bond. & Sing. The Thelephorineae, just as other main groups in the Aphyllophorales, can be divided into families with resupinate carpophore and smooth hymenial surface, pileate carpophore and smooth or rugose-venose hymenophoral surface (*Thelephora*, and probably *Polyozellus*), spinose hymenophore (*Sarcodon* and allied genera), and with poroid hymenophore (*Boletopsis*). What Fayod says about the relationships with certain boletes should not be taken into consideration since there are no such boletes that are related to any Aphyllophorales.

*Botrydina* Bréb., *Mem. Soc. Acad. Sc. Arts & Lett. Fallaise* p. 3. 1839. While it is now obvious that *B. vulgaris* Bréb. is not simply an algal genus (as which it was published) but a dual organism, undoubtedly a basidiolichen, it cannot be established now whether it had an *Omphalina* or a *Gerronema* or some other basidiomycetous fungus as symbiont (see also chapter III, p. 13 and under *Omphalina* and *Gerronema*).

*Cantharellius* Adans. ex Fr., *Syst. Mycol.* 1: 316. 1821. The lectotype is *Cantharellus cibarius* Fr. Many species belong in other genera (*Craterellus*, *Geopetalum*, *Hygrophoropsis*, *Cantharellula*, *Gomphus*, *Leptoglossum*, *Gerronema*); additional species have been described since 1821 which are undoubtedly good species of *Cantharellus* sensu str. These are: *Cantharellus cinnabarinus* (Schwein.) Schwein.; *Cantharellus guyanensis* Mont.; *C. odoratus* (Schwein.) Sing. (*Craterellus odoratus* Schwein.); *C. lateritius* (Berk.) Sing.\* (*Craterellus lateritius* Berk.; *Thelephora cantharella* Schwein.; *Craterellus* Fr.). The last two species have practically smooth hymenial surface but are otherwise very close to *Cantharellus cibarius*. The spore print is always bright colored in *Cantharellus*, mostly yellow or pink. The basidia are long, with often more than 4 sterigmata, and stichic. This genus is the type genus of a small family, Cantharellaceae, consisting of *Cantharellus* and *Craterellus*, the latter containing - not necessarily the smooth - but the thin forms with more cartilaginous trama, the hyphae lacking clamp connections. Typical for these thinner forms is *Craterellus cornucopioides* (L. ex Fr.) Pers. Somewhat intermediate between *Cantharellus* and *Craterellus* is, according to external characters, *Cantharellus minor* Peck; the type (?) possibly a *Hygrocybe* (Petersen, *Mycologia* 68: 315. 1976). Further investigations will certainly show its definite place. The Can-

\**Lilloa* 22: 721. 1951. A.H. Smith published this as a "new" combination (*Mich. Bot.* 7: 159. 1968).

tharellaceae may be interpreted as containing only these two genera and being stichobasidial in all species, or else they may be understood in a wider sense including the *Gomphoideae* (genera with chiastobasidia). In either case, they are not related to the Agaricales but the Clavariineae: *Cantharellus* and *Craterellus* to *Clavulina*, and *Gomphus* to *Ramaria*.

*Caripia* O. Kuntze, *Rev. Gen. Pl.* 3: 451: 1898. The type species is *Caripia montagnei* (Berk.) O. Kuntze. This species is often indicated as *Hypolyscus montagnei* Berk. However, Berkeley was wrong using Persoon's generic name *Hypolyscus* for his tropical American species as was correctly shown and remedied by O. Kuntze. The genus *Caripia* is one of the most interesting forms of the neotropics. It is rarely found in sporulating condition, but the author was able to discover a good specimen from Panamá with fertile hymenial surface. This specimen was compared with the type and with authentic material.

The spores are smooth, ellipsoid, with suprahilar appplanation, heterotropic, hyaline to stramineous-hyaline, inamyloid,  $4.8\text{--}5.8 \times 2.2\text{--}3$ , mostly about  $5.3 \times 2.7 \mu\text{m}$ ; basidia clavate,  $21 \times 5.3\text{--}5.5 \mu\text{m}$ , sterigmata not seen, without septa; cystidia none; surface of the "pileus" sterile, but no cuticle differentiated, and no dermatocystidia or other specialized bodies present; tissue of the upper portion of the carpophore consisting of irregularly intermixed, thick-walled hyphae which are inamyloid. Monomitic. In spite of the fact that this fungus has often been compared with the agarics, or considered as close to them, the author is convinced that it belongs in the stereoid fungi together with *Cotylidia*, *Cymatoderma*, *Skepperia*, and similar genera.

*Chaetotypha* Corda in Sturm, *Deutschl. Flora* 3(2): 133. 1829, with the type *C. variabilis* Corda has been identified with *Cellypha goldbachii* (Weinm.) Donk by Fries and would thus be an older name for *Cellypha*, but Donk (1951) does not consider the two fungi identical and thinks that *Chaetotypha* is not a Basidiomycete. Judging by the original description and illustration (pl. 63) this is apparently a Hyphomycete as has been confirmed by Dr. Dennis (viva voce) who thinks it is *Volutella ciliata* (A. & S.) Fr.

*Cheilophrubium* Opiz & Gintl apud Opiz, *Lotos* 6: 107. 1857. The type and only species, *C. villosum* Opiz from Bohemia, is described as showing ribs (on the underside?) of the pileus starting from the margin and ending half-way to the stipe; ribs all equal and simple, and partly ladder-like-anastomosing; pileus fleshy, yellowish and hirsute; stipe yellowish, glabrous. This may be any kind of an immature agaric from a *Hemimycena* to a *Polyporus*. A *nomen dubium*, since no specimens available.

*Chlorocyphella* Speg., *An. Mus. Nac. Bs. As.* 19: 219. 1909. This is not a Basidiomycete but a lichenicolous parasymbiont; the type of the genus is now (Santesson, *Symb. Bot. Ups.* 12: 41. 1952) called *Pyrenotrichum splitgerberi* Mont. (*Fungi Imperfici*, *Sphaeropsidales*).

*Chloroneuron* Murr., *Mycologia* 3: 25. 1911 is merely a new name for the following genus.

*Chlorophyllum* Murr., *North Am. Fl.* 9: 172. 1910, non Massee (1898). This genus is based on *C. viride* (Pat.) Murr. (*Nevrophyllum viride* Pat.). Murrill's generic name is a homonym, the type species is not an agaric. See also genera *Chloroneuron*, *Gomphus*, and *Nevrophyllum*.

*Clavogaster* Henn., *Hedwigia* 35: 303. 1896. This is identical with *Weraroa* Sing. according to Horak and, if so, has priority. A secotiaceous genus of the southern hemisphere, close to the Strophariaceae of the Agaricales.

*Clavulinopsis* Van Overeem, *Bull. Jard. Bot. Buitenzorg* III. 5. 278. 1923. This is a clavariaceous genus. It must have slipped by mistake into the genera of Agaricaceae (Clements & Shear).

*Collyria* Fr., *Summa Veg. Scan.*, p. 340. 1849. According to Patouillard, this genus was probably established for a monstrosity of the type *Stylobates* (see under that genus, below). If this is correct, it would have to be rejected according to Art. 71 which was, however, deleted by the Leningrad Congress.

*Coriscium* Wainio, *Acta Soc. Fauna Flora Fenn.* 7: 188. 1890. The type is *Endocarpum viride* Ach. (1810) from England. It is difficult to state that this is necessarily the same basidiolichen which was later transferred by Wainio to *Coriscium*, but if so, it is only known as a basidiolichen whose fungus is now classified as *Gerronema*. The interdependence of alga and fungus and the generic identity of the fungus may not be constant in this genus, and the genus may be interpreted as an imperfect lichen since we do not know whether the fungus fructifies normally and regularly. Additional lichenological studies are necessary in order to substantiate the claim that *Coriscium* is always the lichenized state of *Gerronema*. If this were so, *Gerronema* would be a synonym of *Coriscium*.

*Cyphellopsis* Donk, *Medd. Ned. Myc. Vereen.* 18-20: 128. 1931, see under *Merismodes*, p. 848.

*Cystangium* Sing. & Smith, *Mem. Torr. Cl.* 21: 67. 1960, see p. 807.

*Daedalea* Pers. ex Fr., *Syst. Mycol.* 1: 331. 1821. This genus has been regarded as being close to *Agaricus* in the Linnean sense by some of the earlier authors. Later authors have referred it to the Polyporaceae, and in spite of various emendations and the transfer of the genus *Polyporus* itself to the Agaricales, *Daedalea* must be considered as belonging to the Aphyllophorales. It is close to *Daedaleopsis*, *Coriolopsis*, *Whitfordia*, and various other genera, including *Xerotus* Fr. (see there), and together with another group (*Coriolus*, *Microporus*, *Trametes*, *Pseudotrametes*, *Lenzites*, etc.), it forms one of the main subdivisions of the polypores, the Coriolaceae. The type species of *Daedalea* is *D. quercina* (L.) Pers. ex Fr. Some species of *Daedalea* are foreign to that genus; *D. elegans* Spreng. ex Fr. is *Whitfordia elegans* (Spreng. ex Fr.) Sing.; *Daedalea confragosa* (Bolt.) Pers. ex Fr. is *Daedaleopsis confragosa* (Bolt.) Schroeter; *Daedalea unicolor* (Bull. ex) Fr. is *Cerrena unicolor* (Bull. ex) Murr.; *Daedalea philippinensis* Pat. is *Diacanthodes philippinensis* (Pat.) Sing. etc. but none of all these is a species of the Agaricales. However, *Daedalea meruloides* Schwein. is *Gyrodon meruloides* (Schwein.) Sing.

*Elmerina* Bres., *Ann. Myc.* 10: 507. 1912, type *E. cladophora* (Berk.) Bres. This

genus has been included in the "Polyporaceae s. str." by Parmasto. In my opinion, it does not belong in the Agaricales fam. Polyporaceae as accepted here but in the Coriolaceae (Aphyllophorales).

*Favolaschia* (Pat.) Henn., *Engler's Bot. Jahrb.* 22: 93. 1895. This genus is not, as assumed by Patouillard, closely related to *Marasmius* (*Androsaceus*) and the *Marasmieae*. If there is any relationship at all, it would be between *Favolaschia* and the *Panelleae*. But even this affinity is at present not actually substantiated. In the author's opinion (cf. *Beiheft Nov. Hedw.* 50: 1-3. 1974) *Favolaschia* is close to *Aleurodiscus* and should be combined with it in a special family, Favolaschiaceae Sing., *Beih. Nov. Hedw.* 29: 380. 1969. *Favolaschia* differs from *Aleurodiscus* and *Gloeosoma* in smooth spores and "poroid" hymenophore. However, *Favolaschia oligopora* Sing. from Colombia has originally a cup-shaped sessile carpophore which becomes obliquely otideoid, eventually developing a pseudostipe and the margin becoming in one or two places lamellarly extended so that 2-5 cupuliform, unistipitate "pores" result. In this species the hymenium originates from a hyphid-palisade and is clearly a catahymenium. This species is clearly intermediate between *Aleurodiscus* and *Favolaschia* but belongs to *Favolaschia* because of the smooth spores. The catahymenium is foreign to Agaricales as far as we know, and justifies the exclusion of the Favolaschiaceae from that order. *Favolaschia* is distinguished from *Campanella* by amyloid spores, pit-like, round pores which at maturity become favoloid; often also by the presence of dendrophyses and gloeocystidia. The type species is *F. gaillardii* Pat.

*Fistulina* Bull. ex Fr., *Syst. Mycol.* 1: 396. 1821. This, together with *Pseudofistulina* and *Fistulinella*, is usually combined into a family Fistulinaceae Lotsy (tribus Fistulineae Schröter; order Fistulinales Jülich) and placed in the Aphyllophorales. As for *Pseudofistulina* O. & K. Fidalgo, this is justified whereas *Fistulinella* is boletaceous (see p. 796). The gelatinizing of the trama in *Fistulina* - I am familiar with *F. hepatica*, *F. endoxantha*, and *F. antarctica* - and the acanthophysoid hairs of *Pseudofistulina* - I have studied material kindly sent by its author and think that *F. radicata* is congeneric\* - suggest that here we have forms of cyphellaceous fungi with a protocarpic false carpophore (the "pileus" and "stipe") which show strong similarities with cyphelloid reduced agarics, particularly *Stromatocyphella* (p. 345), and perhaps with such protocarp-producing groups as *Syncyphella* (p. 338) and the genus *Mycoalvimia* (p. 433). It appears probable therefore that the Fistulinaceae should be added as a further family close to the Tricholomataceae of the Agaricales. I am not at present ready to introduce Fistulinaceae as a family of the Agaricales, because I believe that additional studies will be required to substantiate this position. It is certain, however, that the Fistulinaceae are very isolated among the polypores and Aphyllophorales.

*Friesula* Speg.; *An. Soc. Cient. Argentina* 8: 284. 1880. This genus is said to be identical with *Skepperia* (see Patouillard, *Essai*, p. 141. 1900). The type species, *F. platenensis* Speg. (l.c.) from Argentina has been studied by the author (see *Lilloa* 23: 123. 1950) and was found to be generically different from *Skepperia*. Its anatomical

\**Pseudofistulina radicata* (Schwein.) Sing. c.n. (*Boletus radicatus* Schwein., *Acta Soc. Nat. Scrut. Lips.* 1: 100. 1822).

characters suggest a position near *Cytidia* and *Skepperia* (both belonging in the Aphyllophorales). However, the final position of this interesting genus should not be prejudged by these results. The possibility of affinity with some tricholomataceous Agaricales has been suggested (viva voce) by Dr. Oberwinkler. Further studies on preferably fresh topotypic material might eventually be provided by Argentine mycologists.

*Galeropsis* Vel. & Dvořák apud Velen. *Mycologia* 7: 106. 1930 (*Psammomyces* Lebedeva 1932, *Cyttarophyllum* (Heim) Sing. 1936) has originally been described as an agaric, but is a secotiaceous fungus of the family Galeropsidaceae (which also includes *Clavogaster* = *Weraroa*). A revision of *Galeropsis* has been published by Singer, Kon. Nederl. Akad. v. Wetensch. Amsterdam. Proc. ser. C66(1): 106-117, 1963. See also Singer & Ponce de León, *Mycotaxon* 14: 82-90. 1982.

*Galerula* Karst., *Bidr. Finl. Nat. Fol.* 32: xxiii. 1879. The type, according to Earle and Murrill is *Agaricus pithyrius* Fr. with uncertain and unascertainable position in the Agaricales. Donk (1941) would have preferred, with some reason, *A. mycenopsis* Fr., itself of somewhat uncertain position. According to Horak (1968, p. 715), Karsten's collections of *Galerula mycenopsis* are ?*Naematoloma udum* (Fr.) Kummer and *Galerina heterocystis* (Akt.) Smith & Sing. (*Hypholoma udum* respectively *G. clavata* in Horak's nomenclature). Thus, even a retypification in Horak's sense makes *Galerula* a genus incertae sedis and a possible synonym with either a strophariaceous or a cortinariaceous genus.

*Gastroboletus* Lohwag ex Keissler & Lohwag in Handel-Mazetti, *Symbolae Sinicae* 2: 54. 1937. The type, *G. boedijnii* Lohwag from China, as well as two additional North American species and an African species have been studied by the present author. The type, according to Horak not existent, is actually preserved (WU) and shows that it represents an independent genus (not a synonym of *Truncocolumella*) of secotiaceous fungi, the type genus of the family Gastroboletaceae Sing., as was anticipated by Singer and Singer & Smith. See also Thiers & Trappe, *Brittonia* 11: 205-223, Singer & Both, *Mycologia* 69: 59-72. 1979, and Singer, *Persoonia* 7: 317-318. 1973; 11: 276-279. 1981. Some authors, e.g. Thiers and Pegler & Young, tend to believe that *Gastroboletus* should enter the Boletaceae because in some species most basidia have the structural appearance of autobasidia and some seem to be close to certain genera of that family. Yet, the basidia do not function as auto-basidia, at least in the type and are accompanied by typical apobasidia (with the sterigmata not curved inwards, half-sickle-shaped). This does not exclude the possibility that some species described in *Gastroboletus* might be products of gasteromycetation or simply growth-inhibited carpophores which did not produce a spore print.

*Gastrocybe* Watling, *Mich. Bot.* 7: 19. 1968 is based on *G. lateritia* Watling (= *Bolbitius rogersii* Heim ad int.) and belongs in the secotiaceous family Galeropsidaceae Sing. 1962 (= *Cyttarophylles* Heim 1968). It comes closest to the agaric family Bolbitiaceae. It occurs in the Middle West of North America and is remarkable by the fact that in contrast to other genera of the same family it is thin-fleshy and gelatinizing and persists only a few hours. I have seen material from Illinois kindly shown

to me by Dr. D.P. Rogers and agree with Watling that "it must be considered a gastromycete in the traditional sense". As for more descriptive data and illustrations see Singer & Ponce de León, *Mycotaxon* 14: 82-90. 1982.

*Gloeocantharellus* Sing., *Lloydia* 8: 140. 1945. The type of this genus, *G. purpurascens* from Tennessee, U.S.A., was first described as *Cantharellus*, and is consequently a former agaric. This is the reason why this genus has been inserted in the list of genera excludenda. *Gloeocantharellus* differs from *Gomphus* and *Chloroneurum* in the presence of gloeocystidia and in more lamellate hymenophore with (in Corner's sense) somewhat (but less) thickening hymenium; it differs from *Linderomyces* in the non-divergent lateral stratum of the hymenophoral trama etc. (see p. 847). *G. okapaensis* Corner (1969) is probably *Linderomyces*, perhaps *L. lateritius* (Petch) Sing.

*Gomphus* S.F. Gray, *Nat. Arr. Brit. Pl.* 1: 638. 1821. The species of *Gomphus*, already distinguished in Persoon's time, were often confused with *Cantharellus* and *Craterellus*, from which they differ in the large spores whose wall becomes rugose after dehydration in the herbarium, or else is rugose, sometimes reticulate-rugose from the beginning (except in immature spores) and strongly cyanophilic; they also differ in the more rugose-venose-reticulate configuration of the hymenophore in most species, chiasmbasidia instead of stichobasidia and have therefore, together with *Gloeocantharellus*, *Pseudogomphus*, and *Linderomyces*, been placed in the family Gomphaceae which, aside from these cantharelloid fungi also contained *Ramaria* (Ramariaceae Corner). *Chloroneurum* Murr. differs from *Gomphus* but little - the spores are perhaps slightly more strongly ornamented and in the type species some cystidia (not pseudocystidia) are present. It may be considered a subgenus or section of *Gomphus* (according to Corner 1966), and Patouillard (1886, 1887, 1900) distinguished under *Nevrophyllum* - a synonym of *Gomphus* - a group (A) without cystidia and a group (B) with projecting cystidia. The latter corresponds to *Chloroneurum*. In a third subgenus, *Gomphorellus*, Corner (1966) indicated the absence of clamp connections. Two species of subgenus *Gomphus* are, according to Corner, also free of clamp connections [*G. canadensis* (Klotzsch ex Berk.) Corner and *G. pseudoclavatus* (A.H. Smith) Corner]; since I have observed very scanty clamp connections in *G. nothofagorum* Sing., it might be desirable to recheck these two species for occurrence of scattered clamps.

*Gramincola* Vel.; *Nov. Myc. Nov., Opera Bot. Cech.* 4: 81. 1947. "Very slender small fungus ... spores globose, small, reddish ..." Based on *G. gracilis* Vel. from Czechoslovakia. No type material existing.

*Helotium*, see p. 400-401.

*Hemigaster* Juel, *Sver. Vet. Akad. Handl.* 21: 111. 1895. This is based on *Hemigaster candidus* Juel. on rabbit dung in Sweden. This fungus is somewhat controversial; the author has not seen any specimens. The fungus is small, passes through a gymnocarpous phase, and becomes then persistently angiocarpous; aside from basidiospores, "gemmae" (probably chlamydospores) are formed; a columella, and a powder, consisting of mature basidiospores and gemmae is found inside the peridium of the adult specimens. This may be a new genus intermediate between

Gastromycetes and Agaricales, or else a gästroid form of some agaric comparable with the gästroid forms of *Suillus decipiens*. In fact, Thaxter who collected this latter in Florida, called his specimens *Hemigaster* sp. Bresadola seemed to think that *Hemigaster* is merely a young stage of a *Coprinus* sp.

*Heteroscypha* Oberwinkler & Agerer, *Sydotia* Beih. 8: 31. 1979. This genus is based on *Cyphella appanata* Talbot but it is not related to *Cyphella* sensu str. i.e. not agaricoid but is considered tremellaceous by their authors.

*Hiatula* (Fr.) Mont., *Ann. Sc. Nat.* IV. 1: 107. 1854. The type, *A. benzonii* Fr. is lost. It may belong to *Mycena* (Tricholomataceae) or *Leucocoprinus* (Agaricaceae); but the latter interpretation is possible only if it is assumed that the specimen, as it reached Fries, has lost its annulus. Material sent to Fries by Oudemans - not the type - belongs, according to Oort (*Med. Ned. Myc. Ver.* 16-17: 249, 1928) to *Leucocoprinus* aff. *cepaestipes* but does not correspond to the description and illustration by Fries and Gonnermann & Rabenhorst since it shows a scaly pileus and an annulus. Consequently, *Hiatula* must be considered to be an agaric of uncertain position. See also p. 511.

Rick distributed material of *Hiatula benzonii*. This material is sterile and is evidently a sterile form of some *Coprinus*. Although Rick's specimens are by no means authentic, they suggest a third possibility viz. that Fries who indicated "sporidia alba" really only noticed white lamellae and that *A. benzonii* was originally nothing but a sterile *Coprinus*. Pegler (1966) indicates that Berkeley's Zanzibar material (K) of *H. benzonii* has characters which would place it in *Lepiota*. Since the original type cannot be found *Hiatula* cannot be placed anywhere in the classification of Agaricales.

*Hybogaster* Sing., *Sydotia* 17: 13. 1964. This is an endocarpous genus belonging in the latex-bearing branch of the Hydnangiaceae (cf. p. 803).

*Hymenogramme* Berk. & Mont., apud Mont., *Syll. Crypt.*, p. 151, 1856. This is based on a species of "Poria", or rather a resupinate representative of the Meruliaceae (polypores), and Saccardo & Cuboni add *Laschia crustacea* (Junguhnia!). This genus as well as *Lenzites* to which it is said to be related, are Aphyllophorales and have nothing in common with the Agaricales except the configuration of the hymenophore. Donk (1964) combines the Meruliaceae with the Corticiaceae whereby *Hymenogramme* becomes a member of the latter family.

*Hypolysssus* Pers., *Mycol. Europaea* 2: 6. 1825. The type species is *H. ventricosus* Pers. This is a combination of an agaric with its parasite, and must therefore be considered either a monstrosity provoked by parasitizing *Hypomyces* (Pyrenomycetes), or else a nomen confusum (its characters deriving from two different genera), according to the Code of 1972. It is impossible to remodel this genus so as to provide the valid name for *Caripia*.

*Laschia* Fr., *Linnaea* 5: 533. 1830. This genus based on *L. delicata*, is a synonym of *Auricularia* (Auriculariales) and has, in spite of the non-smooth hymenophore, nothing to do with any holobasidial group. However, *Laschia* in the sense of Lloyd is the sum of *Filoboletus* (Tricholomataceae) and *Favolaschia* (see above). *Laschia*

*Jungh.* is a later homonym of *Laschia* Fr. and its type species, *L. crustacea* Jungh. is also the type species of *Junghuhnia* Corda em. Ryvarden (*Persoonia* 7: 17-21. 1972). According to him, the type species of *Chaetoporus* is also *Junghuhnia*, but *Chaetoporus* Karst. sensu Bond. & Sing. is *Oxyporus*. Neither *Auricularia*, nor *Junghuhnia*, nor *Chaetoporus* nor *Oxyporus* have any affinity with Agaricales.

*Lentinellus* Karst., *Bidr. Finl. Nat. Folk* 32: xviii. 1879, was treated under Tricholomataceae, trib. Leucopaxilleae in the second edition of the present work, but Maas Geesteranus (*Kon. Nederl. Akad. v. Wetensch. Amsterdam* ser. C. 66: 427. 1963) showed convincingly that its affinities are with *Auriscalpium* S.F. Gray, a "hydnaceous" genus. He proposed a new family Auriscalpiaceae Maas G. for both these genera. It is not yet fully established whether this family is rather aphylophoraceous or referable to the Agaricales. I believe it to be aphylophoraceous because no other genus or species with spinose hymenophore is known in the Agaricales. The only families of Agaricales where dimitic (generative and skeletal hyphae) hyphal structure is known are the Bondarzewiaceae, Russulaceae (one species), and the Polyporaceae, all apparently unrelated to the Auriscalpiaceae. While the former shares with *Auriscalpium* the amyloid ornamented spores, it differs strongly in the spore size, ornamentation, the clamp-less hyphae and the tubular hymenophore, parasitic rather than saprophytic relation to the host plants and generally completely different habit; likewise the type of pseudocystidia present in *Bondarzewia* is different from that of *Lentinellus*. Also, the Auriscalpiaceae show not the slightest indication of affinity with Hydnangiaceae or any other secotiaceous fungi. As for the scope of *Lentinellus* see 2nd ed. p. 299-301. *Hemicybe* Karst. and *Lentaria* Pilát are synonyms.

*Lenzites* Fr., *Gen. Hymen.* p. 10. 1836. With *L. betulina* (L. ex Fr.) as type species, this genus belongs in the Aphylophorales, Coriolaceae. In spite of the lamellae, it is not related to any group of Agaricales.

*Leptomyces* Mont., *Syll. Crypt.* p. 128. 1856. The type has been lost; it could not be found at PC. From the description, it would seem that it belongs in *Mycena* sect. *Radiatae*. Since we cannot prove this identity, the genus is indicated with a "?" among the synonyms of *Mycena*.

*Linderomyces* Sing., *Farlowia* 3: 157. 1947, introduced as paxillaceous, is a gomphaceous genus (see also pl. 31 and p. 126).

*Lyophyllopsis* Sathe & Daniel, *Agar. (Mushr.) Kerala St. MACS Monographs* 1: 87. 1980. The type *L. keralensis* Sathe & Daniel has unfortunately not been studied by the present author. It is said to have siderophilous basidia, white spore print, strongly amyloid spores with cyanophilous ornamentation, hyphae without clamp connections. Taken at face value, this fungus would indeed require separation from other genera, with uncertain taxonomic position; but it may refer to *Melanoleuca*.

*Macowanites* Kalchbr., *Hedwigia* 15: 115. 1876, see p. 807-808.

*Mapea* Pat., *Bull. Soc. Myc. Fr.* 22: 46. 1906. I have studied the type, *M. radiata* Pat. which is, as has been said before by Maire, not an agaric but an atypical rust. Höhnel once identified *Mapea* with *Marasmius corbariensis* Roumégue but re-

pudiated his own statement later. *Mapea* represents the *Uredo*-state of what is now known as *Telomapea* Laundon (1967).

*Merismodes* Earle, *Bull. N.Y. Bod. Gard.* 5: 406. 1909. This cyphelloid genus is based on *Cantharellus fasciculatus* Schwein. This genus was, upon a suggestion by Donk, inserted in the Agaricales in an earlier edition of the present work, but since the affinities with the Crinipellinae seemed doubtful it was later (1962, 2nd ed.) excluded but tentatively re-instated with supposed relationships to the cyphelloid Crepidotaceae (1975). In the meantime, very careful and detailed studies by Agerer on this and related genera\* have convinced me that at the present time any link with Agaricales is speculative and not better founded than any tentative derivation from Aphyllophorales. Regardless whether *Cyphelopsis* Donk is or is not congeneric with *Merismodes*, the former genus is in the same situation. So is *Rectipilus* Agerer, at least the type species. We agree with Agerer & Oberwinkler (1979) in that "the cyphelloid organization of the fruiting bodies in Higher Fungi is widespread. ... In the Basidiomycetes disciform carpophores with central attachment to the substratum are known in Auriculariales, [Tremellales], Dacryomycetales, Aphyllophorales, and Agaricales." The precise point where cyphelloid Agaricales and cyphelloid Aphyllophorales must be separated is difficult to decide inasmuch as authors seem to be influenced by their basic attitude to Basidiomycete phylogeny instead by the possibilities of finding a convincing hiatus between both groups on this level, or by the construction of series linked by demonstrable affinities.

*Montagnea* Fr., *Gen. Hym.*, p. 7. 1836. Many authors consider this genus as belonging to the Agaricales, somewhere near *Coprinus*. There is no doubt in the author's mind but that *Montagnea* is, indirectly, related with the Coprinaceae. However, if there is such a thing as a Gastromycete, *Montagnea* is one of them. It is the type genus of the family Montagneaceae (cf. Singer, *Rev. Myc.* 40: 57-64. 1976).

*Montagnites* Fr., *Epicrisis*, p. 240. 1838. This is a synonym of *Montagnea*. As for the nomenclatorial aspect of the *Montagnites*-problem, see Montagne, *Syll. Crypt.*, p. 130. 1856.

*Mycenopsis* Vel., *Nov. Myc. Nov. Opera Bot. Cech.* 4: 35. 1947. No generic description is given, but the only species, *Mycenopsis globispora* Vel. from Czechoslovakia, is described. The description is insufficient according to modern standards in the *Mycena* group (to which this fungus is supposed to belong), and type material is not available.

*Mycomedusa* Heim ex Heim, *Rev. Myc.* 30: 232. 1965 was introduced for *M. guineensis* Heim. According to Pegler & Rayner it is probably identical with *Favolaschia tonkinensis* (Pat.) Sing. It is certainly not a genus of Agaricales.

*Naucoria* Kummer, *Führ. Pilzk.*, p. 22. 1871. This, according to key characters, coincides with *Naucoria* (Fr.) Quél., *Champ. Jura Vosg.*, p. 131, 1872-73 (*Agaricus* trib. *Naucoria* Fr., *Syst. Mycol.* 1: 260. 1821). It is difficult to decide which species

\*Agerer, R., *Rectipilus, Persoonia* 7: 389-436. 1973; cyphelloide Pilze aus Teneriffa, *Nov. Hedw.* 30: 295-335. 1978; Typusstudien an cyphelloiden Pilzen IV, *Mitt. Bot. München* 19: 163-334. 1983; Agerer, R., H.-J. Prillinger & H.-P. Noll, Studien zur Sippenstruktur der Gattung *Cyphelopsis*, *Zeitschr. Mykol.* 46: 177-207. 1980.

is acceptable as type of the genus. As Donk has argued, any genus based on Fries 1821 would be typified by a species of sect. *Genuini* Fr., more precisely *A. escharoides*, *conspersus*, *siparius*, *pannosus*, *graminicola*, *furfuraceus*, *segestrius*. Unfortunately, the species which has been selected by Donk, *A. escharoides*, is a doubtful species which has been interpreted in a different manner by different authors, viz. as a *Tubaria* near *T. furfuracea* by Ricken, and as *Alnicola melinoides* by others. Secretan (1833) was the first to give an emended description but this refers to var. *naucosus* Fr., not to the type variety, and is perhaps a *Cortinarius*, Ricken's interpretation is by no means certain but probably easier to defend than that adopted later by some French authors inasmuch as Fries's original diagnosis speaks of a carpophore which is "entirely pallid, also in fresh state" and lamellae which are sub-decurrent, later seceding (separating from apex of stipe), broad, buffish pallid, and pileus almost fleshy. There can be no doubt whatsoever that the original *A. escharoides* is a species which might be a *Tubaria*, but might as well be almost anything, not necessarily a cortinariaceous or crepidotaceous fungus. Since the first (legal) lectotype should be accepted, we have little choice but to follow Donk, but we regret that another one of the classical genera will therewith become a nomen dubium. We have consequently (with A.H. Smith, and in a later discussion in *Schweiz. Zeitschr. Pilzk.* 29: 213, 228, 1951) attempted to save *Naucoria* by proposing a lectotype which would preserve *Naucoria* and at the same time save other well-introduced and current generic names of agarics, by appointing for *Naucoria* Kummer the lectotype independently from tribus *Naucoria* Fr. Our choice was *N. centunculus*. However, reading Kummer's key carefully, one must come to the conclusion that his descriptive data ("mit anfangs eingebogenem Rand, etwas fleischig, biscuitartig, Stiel meist zäh-knorpelig") coincide too much with Fries's original diagnosis, and the species indicated are so much the same (with some additions which are not fully in agreement with this description) that it is indeed difficult to appoint a different type species for Kummer's genus, inasmuch as precisely *N. centunculus* has the least incurved margin and the least tough-cartilaginous stipe. Accepting, then, Donk's choice (which has also been the choice of other modern authors) we are sorry to find no legal way to save *Naucoria* (other than conservation - a procedure which might not be successful when it comes to a vote, and which has too few valid arguments in its favor excepting the sentimental satisfaction of having another "classical" generic name maintained). *Naucoria* Kummer and *Naucoria* (Fr.) Quél. [or *Naucoria* (Fr.) Kummer, if one prefers] is therefore a nomen dubium, ambiguous between Cortinariaceae and Crepidotaceae.

*Nevrophyllum* Pat., *Hym. Eur.*, p. 129. 1887. This is a synonym of *Gomphus* (see there).

*Notholepiota* Horak, *N.Z.J. Botany* 9: 479. 1971. This is a secotiaceous fungus based on *N. areolata* (Cunningham) Horak from New Zealand with affinities with the Agaricaceae, evidently related to *Endolepiotula* Sing.

*Panaeolopsis* Sing., *Beih. Nova Hedwigia* 29: 367. 1969. This is a secotiaceous genus which does not shed spores, and similar to and related with the genus *Panaeolus*. It belongs in the Montagneaceae.

*Perona* Pers., *Mycologia Europaea* 2: 3. 1825. Albertini & Schweinitz wrote in a note (p. 351. 1805) that one of their sections of *Helotium* is not typical for that genus and should perhaps better be taken into a separate genus. This is what Persoon did in 1825. He added two species described by Tode. *Perona* is a homonym.

*Phaeomycena* Heim ex Sing. & Digilio, *Lilloa* 25: 175. 1953 ("1951"). This African genus is based on *Phaeomycena aureophylla* Heim ex Heim. When validated it was incorrectly emended to include a species (*P. macrospora* Sing. in Sing. & Digilio) now considered to be a species of *Gerronema*. Type studies by Horak (1968) state that the type material has been damaged. Nevertheless, Horak was able to give the following details: Spores oboval to elliptical, with broad lateral [hilar] apiculus, without suprahilar depression, in KOH with brownish to ocher intraparietal pigment, neither amyloid nor pseudoamyloid, thick-walled, without germ pore, smooth,  $7-8 \times 5-5.5 \mu\text{m}$ ; cheilocystidia not observed; pleurocystidia none; lamellae widely emarginate-adnate and short-decurrent, reticulately intervenose, light orange to brown, with smooth concolorous edge; hyphae of the trama of the hymenophore not differentiated in the material, regular according to Heim (1945); pileus flat-semiglobose, soon repand with straight, smooth, recurved margin, with broad umbilicate umbo, dark red-brown to sordid orange-brown, orange towards the margin which is transparently reticulate-striate, in the center with  $\pm$  radial veins and ribs and viscid, otherwise dry, 35-50 mm broad; cuticle hymeniform, consisting of broadly fusiform or clavate cells which are thin-walled and smooth, with brown vacuolar pigment, no clamp connections observed,  $25-50 \times 13-19 \mu\text{m}$ , no dermatocystidia; stipe central, solitary, cylindric, widened at apex and base, dry, densely pruiniate, velutinous, hollow,  $27-40 \times 2.5-3.5 \text{ mm}$ ; dermatocystidia on stipe narrowly clavate to rounded-cylindric, thick-walled, metuloid, in KOH with reddish brown intraparietal pigment, also with some pigment incrustations,  $80-130 \times 5-8 \mu\text{m}$ , veil none, base of stipe "abgebissen" ("en pied d'éléphant"); context orange brown in the center of the pileus, orange towards the margin, tough. On decayed wood. The only genus where all the reported characteristics of this species would fit is *Agrocybe*, and even there the tough consistency is out of place. At face value, this is a good genus, but at present it cannot be inserted in any of the families of Agaricales. It may belong in the *Tricholomataceae* (near *Oudemansiella*), if it were permitted to assume, as Singer & Digilio did, that the spores are only becoming slightly colored in the herbarium and that the spore print is white or whitish; since Heim placed the genus in the Mycenae, one might assume that he also thought it to be related to white-spored agarics. However, the species may be bolbitiaceous or agaricaceous if the spore print is colored. Other data now missing, but essential for a final disposition of this interesting genus are the exact color of the spore print, the exact structure of the base of the stipe (insititious?), the character of the tramal hyphae, the presence or absence of cheilocystidia, the degree of gelatinization of the epicutis.

*Phlebophora* Lév., *Ann. Sc. Nat.* II. 16: 238. 1841. Hymenophore venose. This is an anomaly common to agarics and according to Patouillard, it is the "cantharelloid" deformation of the white-spored agarics. The type species was found near

Paris and named *P. campanulata* Lév. Quélet says that it is the deformation of *Tricholoma resplendens*. Later additions to the genus are aphylophoraceous (see also under *Vanromburghia*).

*Phlebophyllum* Heim, *Cah. d. l. Makobé* 6: 86. 1968 ex Heim, *Rev. Myc.* 33: 380. 1969. This is based on *P. vitellinum* Heim & Gilles from Gabon, a very interesting, somewhat cantharelloid fungus described as an "agaric" but of "somewhat enigmatic" taxonomic position according to Heim (1968). The data missing in the diagnosis (structure of the epicutis, amyloidity of the hyphae, presence or absence of clamp connections, data on more abundant spores and spore print color, if a spore print is formed, siderophilous granulation present or absent in the basidia, dermatocystidia, etc.) should be supplied to make it possible to decide whether this is a tricholomataceous fungus. Superficially, it looks somewhat like *Filoboletus*.

*Plicaturopsis* Reid, *Persoonia* 3: 150. 1964. This genus is based on *Plicatura crispa* (Pers. ex Fr.) Rea, a meruliaceous species which has been confused with agarics in the past. An agaric genus, *Pleurotopsis* (*Marasmius spodoleucus*) has also been confused with forms belonging to *Plicaturopsis* since misdetermined specimens of *M. spodoleucus* were congeneric with *Plicaturopsis*, yet the type of *M. spodoleucus* is congeneric with *Hohenbuehelia*. Reid (l.c.) considers *Plicaturopsis* as generically different from *Plicatura* - also a meruliaceous genus.

*Polyozellus* Murr., *N. Am. Fl.* 9: 171. 1910. The type species, *P. multiplex* (Underwood) Murr. has thelephoraceous spores and belongs in the Thelephorineae (Aphylophorales) as was first stated by Singer (1951) and later confirmed by Imazeki and Donk.

*Polyporoletus* Snell, *Mycologia* 28: 467. 1936. The type is close to *Scutiger* and was as such identified by Singer, Snell & White, *Mycologia* 37: 124-128. 1945. It is not a bolete.

*Porolaschia* Pat., *Essai* p. 138. 1900. The type of this genus is congeneric with *Favolaschia* (see there).

*Pseudogomphus* Heim, *Rev. Mycol.* 34: 344. 1970, with the type *P. fragilissimus* Heim & Gilles differs from *Gloeocantharellus* by the absence of clamp connections and gloeocystidia. It belongs in the Gomphaceae.

*Pseudohygrophorus* Velen., *Nov. Myc.* p. 28. 1939. Based on *P. vesicarius* Velen. from Chechoslovakia. No type specimens have been found; the position of this genus remains doubtful.

*Ptychella* Roze & Boudier, *Bull. Soc. Bot. Fr.* 26: lxxiv. 1879. This is based on *Ptychella ochracea* Roze & Boudier, a fungus which, according to its authors, "has the external habit, appearance and color of" *Agrocybe pediades*, especially when young but the lamellae are those of *Cantharellus*, *Nyctalis*, etc. This is, also according to Patouillard, a not uncommon monstrosity of brown-spored and black-spored agarics; in this particular case, it is probably a phlebophoroid aberration of *Agrocybe vervacti*, a species not uncommon in France.

*Raddetes* Karst., *Hedwigia* 26: 112. 1897 "a gelatinous, stipitate fungus; hymeno-

phore continuous with the stipe, descendent into a minutely cellular trama; stipe central, lamellae simple, attingent; partial veil floccose-glutinous, thin". Karsten. This genus is based on *R. turkestanicus* Karst. from Ashkhabad, Middle Asia. The pileus is said to be subcampanulate-cylindric; spores were not seen. Lebedeva compares her *Psammomyces* (i.e. *Galeropsis*) with *Raddetes* but the spores are too obvious in any secotiaceous fungus to be overlooked. Saccardo identifies it with *Stylobates* which is not a great help since *Stylobates* is just as puzzling as *Raddetes*. Recent revisions of *Raddetes* in the U.S.S.R. appear to prove that *Raddetes* is a dacryomycete.

*Rectipilus* Agerer, *Persoonia* 7: 413. 1973. The type, *R. fasciculatus* (Pers.) Agerer, belongs in a group with inamyloid hairs. Thus defined, it does not show any demonstrable affinities with Agaricales, and seems to be allied to *Henningsomyces* which most authors consider as belonging in the Aphyllophorales.

*Rhodoarrhenia* Sing., *Sydotria* 17: 142. 1964. The genus is based on *Merulius pezizoides* Speg., a species which has the external appearance of *Arrenia auriscalpium* and a comparable development, but certainly not the same or similar characters and no affinity with the Omphalinae of the Tricholomataceae. The other species described in *Rhodoarrhenia* are also easily taken for agarics. They are tropical species which I consider meruliaceous rather than tricholomataceous.

The genus *Rhodoarrhenia* can be characterized by the gelatinized trama of the pileus-cup, small to medium (to 9 µm) spores which are often colored in print (cream, red), the branching thin hyphae of the surface of the sterile side of the cup and the stipe but the absence of a *Rameales*-structure or asterostromelloid structure, the even (short-elliptic to subcircular, or elliptic) outline of the spores, absence of cystidia of any sort, the nutant pileus-cup, and the white but yellowing, fulvescent, reddening or salmon yellow staining surfaces remove it from tricholomataceous forms. Here: *R. pezizoides* (Speg.) Sing. (*Merulius*, Speg., Rimbachia, Lloyd; *Arrenia*, Pat.); *R. albocrenea* Sing.; *R. nobilis* Sing.; *R. flabellulum* (Berk. & Curt. ex Cooke) Sing. (*Favolus*, Berk. & Curt., ined.; Laschia, Cooke; *Arrenia*, Dennis); *R. cyphelloides* (Lloyd) Sing. (*Rimbachia*, Lloyd); *R. vitellina* (Lloyd) Sing. (*Rimbachia*, Lloyd).

*Richoniella* Cost. & Dufour, *Nouv. Fl. Champ. Fr.*, p. 203. 1891. This is based on *Hymenogaster leptoniisporus* Richon, a species with hymenogastraceous features, but with spores reminiscent of those of *Entoloma*, i.e. obtusely angular and reddish when mature. This is clearly a Gastromycete, but with probable distant affinity with the Entolomataceae. It has been introduced - erroneously in my opinion - as a genus of the Entolomataceae (Rhodophyllaceae, Agaricales) by Romagnesi (1957 and previous papers) an arrangement which can - and should - only be interpreted as an emphatic re-affirmation of the phylogenetic relationship between these two genera, first discovered by Romagnesi.

*Schizophyllum* Fr., *Syst. Mycol.* 1: 330. 1821. This genus has been treated by most authors including the present author (1951, 1962) as a representative of the Agaricales. The reader is referred to the second edition of this work (1962) p. 179-180.

It was then stated that this disposal of *Schizophyllum* represents only a temporary solution. Donk (1964) has pointed out that *Schizopyllum* has indeed affinities among the Aphyllophorales - the genera *Stromatoscypha* Donk and *Henningsiomycetes* O. Kuntze - and that the ontogenesis of the "gills" in *Schizophyllum* (cf. also Essig, *Univ. Calif. Publ. in Bot.* 7: 447-498. 1922) is so peculiar that homology with the lamellae of the Agaricales on account of these structures alone is out of the question. One may add that the consistency of *Schizophyllum* is different from that of other Agaricales. Donk recognized therefore a family Schizophyllaceae Roze (as Schizophyllacées), Quél. (as *Schizophyllei*) in the Aphyllophorales. The present author agrees with this disposition. *Apus* Nees ex Gray, *Schizonia* Pers., *Rhipidium* Wallr., *Hyponeuris* Paulet ex Earle and *Schizophyllum* Fr. ex Murr. are synonyms.

*Secotium* G. Kunze, *Flora* 23: 321. 1840. The type genus of the Secotiaceae (Gastromycetes), is based on *Secotium gueinzii* G. Kunze from South Africa. This and related genera (Secotiaceae) have been studied carefully on the basis of type material by A.H. Smith and Singer (see *Madroño* 15: 152-158. 1960); *Secotium* is related to the Agaricales, particularly the Agaricaceae, as has been foreseen by some authors but belongs in the family Secotiaceae (Gastromycetes) which we consider a natural unit leading not only to agaricaceous but probably also lycoperdaceous groups.

*Semiomphalina* Redhead, *Can. Journ. Bot.* 62: 886. 1984. This genus is based on *Pseudocraterellus leptoglossoides* Corner, a species unknown to me. It appears to be a good genus characterized by the total absence of a hymenophore, pleurotoid-spatuloid habit, lack of clamp connections on the remarkably swollen (to 22 µm according to Corner) hyphae, and the lichenization observed by Redhead. It may indeed be interpreted as a reduced form related to *Gerronema* but it should also be kept in mind that *Botrydina*-like lichen thalli are likewise formed by certain Aphyllophorales and that the inflation of carpophore hyphae is not a valid means of differentiation between Aphyllophorales and Agaricales. In Agaricales, lichenization is not a sufficient reason for generic separation unless accompanied by other distinctive, diagnostic characters.

*Skepperia* Berk., *Trans. Linn. Soc., London* 22: 130. 1859. If the type species is *S. convoluta* - and it is impossible to consider any other species as such -, *Skepperia* cannot be considered as a genus of the Agaricales as has been suggested by Patouillard. The palisadic layer on the outside of the convolute mitruloid carpophore consists of inflated, round bodies with a deeper colored inner, and a colorless outer layer of the wall in the upper portion; the hyphae are inamyloid and with clamp connections; the basidia are rather long, with the lower portion often decurved; spores were not found in the type specimen at the Farlow Herbarium. It shall not be denied that perhaps some other species described in *Skepperia* have closer relations with the Agaricales, but it is the author's conviction that *Skepperia convoluta*, and thus the genus *Skepperia*, is a stereaceous fungus, i.e. it belongs in the family Stereaceae, together with *Caripia*, *Cymatoderma*, etc. These Stereaceae are to the Coriolaceae, what the Thelephoraceae are to the Boletopsidaceae, i.e. differing mainly in smooth hymenial surface. A species more recently described as a European *Skepperia* is *Cotylidia carpatica* (Pilát) Huijsman, also aphyllophoraceous.

*Sphaerobasidioscypha* Agerer, *Mitt. Bot. München* 19: 294. 1983. The genus is based on *S. citriospora* Agerer which, as Agerer emphasizes, shares globulose-clavate basidia only with a second species of the same genus, not, however, with any other cyphelloid genus. In spite of the pseudoamyloid, incrusted hairs, it would seem that there is no demonstrable affinity with cyphelloid genera belonging to the Agaricales. The shape of the basidia is probably rather like that of some Aphyllophorales.

*Stylobates* Fr., *Afzel. Fung. Guian.*, p. 5, 1837. The diagnosis of this genus is bewildering, and if *S. paradoxus* Fr. is recognized as type species, it is impossible to tell what Fries had in his hands when describing this fungus. It may just as well have been an aberrant form of some agaric, as Patouillard thinks, as it may have been a representative of some other order. Perhaps there is some material available for further study. Meanwhile, the best one can do is accept, on a temporary basis, Patouillard's statement (*Essai*, p. 177): "Anomaly of agarics where the lamellae are continued on the upper surface of the pileus where they anastomose more or less instead of being limited to the lower surface of the pileus." *S. paradoxus* was collected in Africa.

*Tilotus* Kalchbr., *Grev.* 9: 137. 1881, nom. prov. ex Sacc., *Syll. Fung.* 5: 652. 1887 is based on *T. lenzitiformis* Kalchbr. ex Sacc. There are no specimens available for study. What I misinterpreted as type is probably a faulty identification by Cooke given to another South African collection - MacOwan 1401 which I considered to be *Phylloptopsis nidulans*, but which was restudied by Reid and identified as *Phylloptopsis salmoneus*. What the original *Tilotus lenzitiformis* was cannot be established without authentic specimens. *Tilotus* is apparently a homonym of *Tylotus* Agardh 1876.

*Tomentifolium* Murr., *Journ. Mycol.* 9: 94. 1903 is based on the same type as *Tilotus* Kalchbr. and is a substitute for it. It is likewise impossible to identify. The original (lost) collection may have been a monstrosity.

*Tubariopsis* Heim, *Le genre Inocybe*, p. 61. 1931. "Pileus thin, hygrophanous, with straight margin, with cellular epicutis formed by subisodiametric elements; stipe inseparable from the pileus, fibrous, fistulose and contorted, elastic; lamellae distant, thick, venose and anastomosing, subdecurrent; spores large, smooth, obovoid, with a broad germ pore, with triple wall, brown; cystidia rare, projecting, not muricate, thin-walled. On the earth." Heim. The type species has a true epithelium, judging from the figure; the septa are drawn without clamps; the cystidia are shown with ampullaceous apex. Madagascar.

Heim later emphasized the dry context which may be comparable with that of *Galeropsis*.

According to the data indicated by Heim and quoted above, this genus differs from *Pholiota* in the large number of globose elements without dermatocystidia in the cuticle, and in the imperfect development of the hymenophore. If *Tubariopsis* is closer to *Galeropsis*, it is certainly well characterized by its epithelium.

The author has not seen the material on which Heim based his description. However, since obviously most of the important characters are indicated, and the fungus does not fit into any of the genera existing until 1931, it may be allowed to accept this genus on the evidence of Heim's description and insert it temporarily among the *Genera incertae sedis*. The type and only species known is *T. torquipes* Heim. It is very probable that this is secotiaceous rather than a true agaric. According to Heim, a type has not been conserved at Paris.

*Tymanopelta* Horak, N.Z.J. Botany 9: 485. 1971. Based on *T. galanthina* (Cooke & Mass.) Horak, this genus is a secotiaceous fungus belonging in the family Galeropsidaceae.

*Vanromburghia* Holtermann, Myk. Unters. Trop., p. 104. 1898. This is based on *V. silvestris* Holtermann from Tjibodas, Java, Indonesia. A topotype is preserved in the Donk Herbarium, Leiden, and was kindly lent to me for study. This material seems to be much more mature than Holtermann's and shows clearly a venose hymenophore. This is a species of *Marasmius*, sect. *Sicci*, close to *M. setulifolius* Sing. from tropical America. I doubt, however, that this is specifically identical with *Phlebophora rugulosa* Lév. in Zollinger (Craterellus, Pat.; Mycena, Höhn) which was described as "tremeloso", "ad terram" nor does this material fully agree with the description of *Vanromburghia rugulosa* (Lév.) Boedijn as described by Boedijn (*Sydowia* 5: 214. 1951) since in our material the setulae-bearing elements are very conspicuous and the basidia shorter, the spores not so broad and the trama not distinctly dimorphic. If the "topotype" of the Herbarium Donk is accepted as representing *Vanromburghia silvestris*, the latter genus becomes a synonym of *Marasmius*. Holtermann's type has not been preserved, or has been lost.

If *Vanromburghia* is, as Hennings thought, the same as *Phlebophora solmsiana*, it is not an agaric but a *Stereum*-like (stipitate *Stereums*) representative of the Aphyllophorales. I have seen the type material (B) of *P. solmsiana* Henn. and am certain that it does not belong in the Agaricales. I have furthermore studied the Javanese specimens (FH) on which Höhn based his transfer of *Phlebophora rugulosa*, generally believed to be conspecific with *Vanromburghia silvestris* Holtermann and find it very much as described by Corner (1966). I agree with Donk (1957) that it is neither marasmoid nor mycenoid. It is, of course, likewise not a species of *Troglia* since its macro- and microscopical characteristics are quite different. It is in my opinion stereoid in the sense that it belongs in or very near the Podoscyphaceae. *Phlebophora solmsiana* Henn., often considered identical with *Vanromburghia silvestris* has more distinctly and more consistently thick-walled hyphae but as long as those of Corner's material, slightly longer spores ( $9.8 \times 5.5 \mu\text{m}$ ) and makes the impression that it is an example of the older stage of *V. silvestris*. However, the cystidia are not as well developed as they are in *P. rugulosa*.

Since all three collections come from Java, Donk's collection (see Singer, *Flora Neotropica* 17: 205. 1976) cannot be given the weight of "the" topotype and *Vanromburghia* must be considered as belonging to the Aphyllophorales.

*Volvella* Gilbert & Beeli apud Gilbert, Notules sur les Amanites (Suppl.), p. 3. 1941.

The type, *Amanita floccosolivida* Beeli, is insufficiently known; it is impossible to decide whether it belongs in Amanitaceae, Pluteaceae or Agaricaceae. See also Horak (1968, p. 616-618).

*Volvoboletus* Henn. in Engler & Prantl, *Nat. Pfl. fam.* I. 1: 196. 1898. This genus is based on *Boletus volvatus* Pers. = *Volvoboletus volvatus* (Pers.) Henn. which includes some species of the Amanitaceae, probably *Amanita* where the lamellae have been transformed into pores by a disease or an abnormality of the hymenophoral structure as can be observed frequently in *Amanita gemmata* in Europe. *Boletium* Clements is based on the same type.

*Xerocoprinus* Maire, *Bull. Soc. Bot. Fr.* 7: ccxiv. 1907, is based on *X. arenarius* (Pat.) Maire (*Coprinus arenarius* Pat.). This differs from *Coprinus* in having lamellae which are only subdeliquescent or non-deliquescent at maturity; pattern of the hymenium not corresponding to that of the inequihymeniferous form; annulus present; cystidia, none; context somewhat toughish as in many Gastromycetes such as *Galeropsis*, *Montagnea*, *Battarea*, etc. In deserts. The development of the carpophores has not been studied, and it may well be that it is hemiediocarpous. This genus has been restudied since Patouillard (1892) and Maire (1907) by Malençon & Bertault (1970) but these authors make no mention of the veil and state that the lamellae are strongly deliquescent. They do not redescribe the structure of the hymenium but their treatment gives to understand that they consider *X. arenarius* a typical representative of *Coprinus*. Horak (1968) on the other hand describes and draws an inferior annulus and denies any gastromycetoid relations. If so, the genus undoubtedly belongs in the Coprinaceae, but more detailed data on (preferably young and fresh) topotypical material will prove or disprove its identity with *Coprinus* or its possible relations with secoziaceous fungi. Missing data are the consistency and the veil of the stipe in its development and anatomy, the exact structure of the hymenium, and the dehiscence or non-dehiscence of the spores (production of a spore print). If it should turn out to be a *Coprinus* after all, it might be near *C. psammonophilus* Speg.

*Xerotus* Fr., *Elenchus Fung.*, p. 48. 1828 (*Xerotinus* Reichenb., *Conspectus Regni Veg.*, p. 14. 1828). The type species is *X. afer* Fr. from Africa. This is preserved at Uppsala from where the author received a fragment and a photograph of the type specimen (Pl. 49,2). Another part of the type (K) was likewise studied. The fragment has some of the anatomical and chemical characters of *Gloeophyllum* but seems to be different from the astipitate *Gloeophyllum* only in the strong development of the stipe and the hyphal system (acc. to Mrs. Kauffmann Fidalgo, 1959). It has not the slightest affinity to those species (of *Anthracophyllum*, etc.) which were later erroneously dumped in the genus *Xerotus*. The true *Xerotis* are close to *Daedaleopsis*, *Gloeophyllum*, *Daedalea*, *Coriolopsis*, etc. - all true polypores (Coriolaceae).

Donk (*Persoonia* 1: 294. 1960) thinks that *Xerotes* and *Xerotus* are merely variant spellings and that *Xerotus* is not a new name for the preoccupied *Xerotes* Fr. non R. Br. as we were used to think. If Donk's interpretation of the homonymy rule is considered to be the correct one, *Xerotus* must be replaced by Reichenbach's new name *Xerotinus* Reichenb., *Conspect. Regni Veg.*, p. 14. 1828.

There are two species known in this genus, *X. afer* (Fr.) Donk and *X. erubescens* (Berk.) Sing. (*Daedalea* Berk.; *Xerotus* Sing. apud Martin; *Lentinus frondosus* Henn.). "*Panus*" *gloeophylloides* Corner is apparently a third one.

*Zephirea* Vel., *Nov. Myc. Nov., Opera bot. Cech.* 4: 61. 1947. "Very slender, vitreous-transparent, non-hygrophanous, evelate, trembling; stipe very long, capillary, smooth, ... Lam. distant, narrow, free. Spores intensely yellow, with the shape of a trapezoid, smooth. Cystidia needle-shaped." Velenovsky. The type species is *Z. fusispora* Vel. from Czechoslovakia. Horak reports on the holotype (PR) that it still exists in minute fragments. His analysis shows that Velenovský based his species on fruiting bodies of a *Mycena* sp. (see also Svrček, *Česká Mykol.* 20: 73. 1966) and spores of a *Clitopilus* and an *Entoloma (Rhodophyllus)* spec. Thus *Zephirea* is a typical nomen confusum according to Art. 70 of the "Seattle Code" 1972 but this article was deleted by the Leningrad Congress 1975. Whatever element of the type is proposed as lectotype, *Zephirea* will be a synonym of an earlier generic name.

*Zerovaemyces* Gorovoy, *Dokl. Akad. Nauk. Ukr. SSR* 8: 746. 1977. See p. 518.

## BIBLIOGRAPHY

- ADAMS, J.F., *Origin and development of the lamellae in Schizophyllum*. - *Mem. Torrey Bot. Club* 17: 326-333. 1918.
- AGERER, R., *Lachnella-Crinipellis, Stigmatolemma - Fistulina: zwei Verwandtschaftsreihen?* - *Zeitschr. f. Mykologie* 44: 51-70. 1978.
- AGERER, R., *Typusstudien an cyphelloiden Pilzen I*, *Zeitschr. f. Mykologie* 45: 191-194. 1979. - III: *Sydotia* 32: 5-12. 1979; IV: *Mitt. Bot. München* 19: 163-334. 1983.
- ALLEN, C.A., *The development of some species of Hypholoma*. - *Ann. Myc.* 4: 387-394. 1906.
- ARAUJO AGUIAR, I. d. J., *Contribuição ao conhecimento da família Cortinariaceae (Agaricales) na Amazonia Brasileira*. - Thesis, Manaus 1985.
- ARDENNE R. v., H. DÖPP & W. STEGLICH, *Über das Vorkommen von Muscaflavin bei Hygrocyben und seine Dihydroazepin-Struktur*. - *Zeitschr. f. Naturforsch.* 29 C: 637-639. 1974.
- ARNOLD, J.D., *A comparative study in certain species of Marasmius and Collybia in culture*. - *Mycologia* 27: 338-415. 1935.
- ARNOULD & GORIS, *Sur une réaction colorée chez les Russules et les Lactaires*. - *Bull. Soc. Myc. Fr.* 23: 174. 1907.
- ARPIN, N. & J.L. FIASSON, *The pigments of Basidiomycetes: their chemotaxonomic interest*, in Petersen (1971), pp. 63-98.
- ARPIN, N. & R. KÜHNER, *Les grandes lignes de la classification des Boletales*. *Bull. Soc. Linn. Lyon* 46: 83-108; 181-208. 1977.
- ATKINSON, G.F., *The development of Agaricus campestris*. - *Bot. Gaz.* 42: 241-264. 1906.
- ATKINSON, G.F., *The origin and taxonomic value of the veil in Dictyophora and Ithyphallus*. - *Bot. Gaz.* 51: 1-20. 1911.
- ATKINSON, G.F., *The development of Agaricus arvensis and Agaricus comtulus*. *Amer. Journ. Bot.* 1: 3-22. 1914.
- ATKINSON, G.F., *The development of Armillaria mellea*. - *Mycol. Centr.-bl.* 4: 113-121. 1914.
- ATKINSON, G.F., *The development of Amanitopsis vaginata*. - *Ann. Myc.* 12: 369-392. 1914.
- ATKINSON, G.F., *The development of Lepiota clypeolaria*. - *Ann. Myc.* 12: 346-356. 1914.
- ATKINSON, G.F., *Morphology and development of Agaricus Rodmani*. - *Proceed. Amer. Phil. Soc.* 54: 309-343. 1915.
- ATKINSON, G.F., *Homology of the universal veil in Agaricus*. - *Myc. C.bl.* 5: 13-19. 1915.
- ATKINSON, G.F., *Origin and development of the lamellae in Coprinus*. - *Bot. Gaz.* 61: 89-130. 1916.
- ATKINSON, G.F., *Development of Lepiota cristata and Lepiota seminuda*. - *Mem. N. Y. Bot. Gard.* 6: 209-228, pl. 21-26. 1916.
- ATKINSON, G.F., *The genus Galerula in North America*. - *Proceed. Amer. Phil. Soc.* 59: 357-374. 1918.
- BAMBEKE, CH. VAN, *Recherches sur les hyphes vasculaires des Eumycètes*. - *Bot. Jaarb. Dod.* 4: 176-239. 1892.

- BAMBEKE, CH. VAN, *Sur la presence de crystalloides*. - *Bull. Ac. r. Belg.* 4: 227-250. 1902.
- BARONI, T.J., *A revision of the genus Rhodocybe Maire (Agaricales)*. - *Beih. Nova Hedwigia* 67: 1-194. 1981.
- BARRON, G.L. & Y. DIERKES. *Nematophagous fungi: Hohenbuehelia, the perfect state of Nemactoctonus*. - *Can. J. Bot.* 55: 3054-3062. 1977.
- BAS, C., *The genus Gloiocephala Massee in Europe*. *Persoonia* 2: 77-89. 1961.
- BAS, C., *The genus Squamanita*. *Persoonia* 3: 331-359. 1965.
- BAS, C., *Morphology and Subdivision of Amanita and a monograph on its section Lepidella*. *Persoonia* 5: 285-579. 1969.
- BAS, C., *A comparison of Torrendia pulchella (Gasteromycetes) with Amanita (Agaricales)*. - *Nov. Hedw. Beih.* 51: 53-61. 1975.
- BAS, C., *Studies in Amanita I*. - *Persoonia* 10: 1-22. 1978.
- BATAILLE, F., *Réactions chimiques sur quelques champignons*. - *Bull. Soc. Myc. Fr.* 47: 106-107. 1931. (Reprint Lehre 1969).
- BATAILLE, F., *Les réactions macrochimiques chez les champignons*, pp. 1-172. Paris 1948.
- BEATON, G., D.N. PEGLER & T.W.K. YOUNG, *Gasteroid Basidiomycota of Victoria State, Australia*. - *Kew Bull.* 39: 499-508. 1984.
- BECK, G. v. MANNAGETTA, *Versuch einer systematischen Gliederung der Gattung Boletus L. em. Zeitschr. Pilzk.* 2: 141-149. 1923.
- BEELI, M., *Flore iconographique des champignons du Congo*. Bruxelles, fasc. 1-2: 1-45, pl. 1-8. 1935.
- BEER, R., *Notes on the development of the carpophore of some Agaricaceae*. - *Ann. Bot.* 25: 683-689. 1911.
- BENEDICT, R.G., V.E. TYLER, Jr., L.R. BRADY & D.E. STUNTZ, *Preliminary chemotaxonomic appraisal of certain Tricholoma species*. *Planta Medica* 12: 100-106. 1964.
- BENEDICT, R.G., V.E. TYLER, JR., L.R. BRADY & D.E. STUNTZ, *Taxonomic status of Pholiota aurea*. *Mycologia* 64: 1167-1169. 1972.
- BENEDIX, E.H. (1963). *Bemerkungen zur Mykorrhiza im System der Boletaceen*. Mykorrhiza. Fischer. Jena.
- BENSAUDE, M., *Recherches sur le cycle évolutif et la sexualité des Basidiomycètes*. - *Rev. gen. Botan.* 30: 1-153. 1918.
- BESL, H.A. & A. BRESINSKY. *A tale told from bolete pigments*. *McIlvainea* 5: 33-38. 1981.
- BESL, H.A. & A. BRESINSKY. *Notizen über Vorkommen und systematische Bewertung von Pigmenten in Höheren Pilzen*. In *Z. Pilzk.* 43: 311-322. 1977.
- BESL, H. A., A. BRESINSKY, L. KOPANSKY & W. STEGLICH. 3-O-methylvariegatsäure und verwandte Pulvinsäurederivate aus Kulturen von *Hygrophoropsis aurantiaca* (Boletales). In *Z. Naturforsch.* 33c: 820-825. 1978.
- BESL, H.A., A. BRESINSKY & I. KRONAWITTER. *Notizen über Vorkommen und systematische Bewertung von Pigmenten in Höheren Pilzen*. In *Z. Pilzk.* 41: 81-98. 1975.
- BESL, H.A., A. BRESINSKY, W. STEGLICH & K. ZIPFEL. *Über Gyrocyanin, das blauende Prinzip des Kornblumenröhrlings ...* *Chem. Ber.* 106: 3223-3229. 1973.
- BESL, H.A., H.-J. HECHT, P. LUGER, V. PASUPATHY & W. STEGLICH. *Tridentochinon ...* In *Chem. Ber.* 108: 3675-3688. 1975.
- BESL, H.A., I. MICHLER, R. PREUSS, W. STEGLICH. *Grevellin D, der Hauptfarbstoff von Suillus granulatus, S. luteus und S. placidus (Boletales)* - *Zeitschr. Naturf.* 29c, 784-786. 1974.
- BESSON, M.A., *Structure de la paroi sporique des Rhodocybe, Rhodotus et Clitopilus (Agaricales)*. *C. R. Acad. Sci. Paris.* 269: 142-145. 1969.

- BESSON, M.A., *Ultrastructure de la paroi sporique amyloïde et ornée de quelques Hyménomycètes*. C.R. Acad. Sci. Paris. 271: 964-967. 1970.
- BESSON, M.A., *Contribution à la connaissance de l'infrastructure de la paroi sporique des Hyménomycètes*. Ph. D. dissertation. Univ. Claude Bernard, Lyon 1972.
- BESSON, M.A. & R. KÜHNER, *Recherches morphologiques et ontogéniques sur la paroi sporique et le pore germinatif des Panaeolus (Fr.) Quel. (Agaricales)*. C.R. Acad. Sci. Paris. 274: 1915-1920. 1972.
- BIGELOW, H.E., *Omphalina in North America*. Mycologia 62: 1-32. 1970.
- BIGELOW, H.E. & J.R. ROWLEY, *Surface replicas of the spores of fleshy fungi*. Mycologia 60: 869-887. 1968.
- BIGELOW, H.E. & A.H. SMITH, *The status of Lepista - a new section of Clitocybe*. Brittonia 21: 144-177. 1969.
- BIGELOW, H.E. & A.H. SMITH, *The genus Clitocybula*. - Mycologia 65: 1101-1116. 1973.
- BIGELOW, H.E. & A.H. SMITH, *Studies in the Tricholomataceae: Hygrophoropsis, Cantharellula, Myxomphalia, Omphaliaster*. - Nov. Hedw. Beih. 51: 61-77. 1975.
- BIGELOW, H.E. & A.H. SMITH, *Notes on Fayodia ss. lato*. - Mycotaxon 9: 38-47. 1979.
- BIGELOW, H.E. & A.H. SMITH, *North American species of Clitocybe I*. - Nov. Hedw. Beih. 72: 1-213, 102 fgs. 1982.
- BLAKESLEE, A.F., *Sexual reproduction in the Mucorineae*. - Proceed. Amer. Acad. Arts Sc. 40: 205-319. 1904.
- BLIZZARD, A.W., *The development of some species of Agaries*. - Amer. Journ. Bot. 4: 221-240. 1917.
- BOEDIJN, K.B., *Beitrag zur Kenntnis der Pilzflora von Sumatra*. - Rec. Trav. Bot. Neerl. 26: 396-439. 1928.
- BOEDIJN, K.B., *The genus Chitonella...* - Bull. Jard. Bot. Buitenzorg III, 13: 276-280. 1934.
- BOEDIJN, K.B., *A poisonous species of Phaeomarasmius (Agaricaceae)*. - Bull. Jard. Bot. Buitenzorg II, 16: 76-82. 1938.
- BOEDIJN, K.B., *Some mycological notes*. - Sydowia 5: 211-229. 1951.
- BOIDIN, J., *Recherche de la tyrosinase et de la laccase chez les Basidiomycètes ...* - Rev. d. Mycol. 16: 173-197. 1951.
- BONDARZEW, A.S. & R. SINGER, *Zur Systematik der Polyporaceae*. - Ann. Mycol. 39: 43-65. 1941.
- BONDARZEW, A.S. & R. SINGER, *K yestestvennoy sisteme trutovykh gribov*. - Sov. Bot. 1943: 29-43. 1943.
- BOTHE, F., *Genetische Untersuchungen über die Lichtentwicklung der Hutpilze*. - Arch. Protistenk. 85: 369-383. 1935.
- BOUDIER, E., *Des champignons*, pp. 1-136, pl. 1. Paris 1866.
- BOURDOT, H. & A. GALZIN, *Hyménomycètes de France*, pp. I-III, 1-761. Sceau 1972. (Reprint Lehre 1969.)
- BOURSIER, J., *Leucopaxillus nov. gen.* - Bull. Soc. Myc. Fr. 41: 391-393. 1925.
- BOURSIER, J. & R. KÜHNER, *Notes sur le genre Inocybe*. - Bull. Soc. Myc. Fr. 44: 170-189. 1928.
- BOUSSET, M., *Un nouveau basidiomycète à acide cyanhydrique*. - Bull. Soc. Myc. Fr. 55: 123-126. 1939.
- BOUSSET, M., *Observations sur le chimism des champignons à l'aide du méthylparamidophénol*. - Bull. Soc. Linn. Lyon 8: 154-158. 1939.
- BREFELD, O., *Untersuchungen aus dem Gesamtgebiete der Mykologie*. - Basidiomyceten III: 280 pp., 11 pl. Muenster 1877; VII: 178 pp., 11 pl. 1888; VIII: 305 pp., 12 pl. 1889.

- BRESADOLA, G., *Iconographia Mycologia*. 27 vol. Mediolani. 1927-41 (vol. 27 by E. Gilbert).
- BRESINSKY, A. *Zur Frage der taxonomischen Relevanz chemischer Merkmale bei Höheren Pilzen.* Travaux dédiés à R. Kühner. Bull. Soc. Linn. Lyon No. spécial: 63-84. 1974.
- BRESINSKY, A. & R. BACHMANN. *Bildung von Pulvinsäurederivaten durch Hygrophoropsis aurantiaca*: Z. Naturforsch. 26b: 1086-1087. 1971.
- BRESINSKY, A. & H. BESL., *Notizen über Vorkommen und systematische Bewertung von Pigmenten in Höheren Pilzen*. Z. Mykol. 45: 247-264. 1979.
- BRESINSKY, A., H. BESL & W. STEGLICH, *Gyroporin und Atromentinsäure aus Leccinum aurantiacum Kulturen*. Phytochemistry 13: 271-272. 1974.
- BRESINSKY, A. & P. ORENDI, *Chromatographische Analyse von Farbmerkmalen der Boletales ... - Z. Pilzk.* 36: 135-169. 1970.
- BRESINSKY, A. & A. RENNSCHMID, *Pigmentmerkmale, Organisationsstufen und systematische Gruppen bei Höheren Pilzen*. Ber. dt. bot. Ges. 84: 313-329. 1971.
- BRESINSKY, A. & G. SCHWARZER, *Mikroskopische Analyse der Hutdeckschichten einiger Agaricales. Boletales and Russulaceae*. - Zeitschr. Pilzk. 35: 263-293. 1969.
- BRESINSKY, A. & P. ORENDI, *Chromatographische Analyse von Farbmerkmalen der Boletales und anderer Makromyzeten auf Dünnschichten*. - Zeitschr. Pilzk. 36: 135-169. 1970.
- BRESINSKY, A. & A. RENNSCHMID, *Pigmentmerkmale, Organisationsstufen und systematische Gruppen bei höheren Pilzen*. - Ber. Deutsche Bot. Gesellschaft 84: 313-329. 1971.
- BRESINSKY, A. & J. STANGL, *Beiträge zur Revision M. Britzelmays "Hymenomyceten aus Südbayern" 13. Die Gattung Melanoleuca...* - Zeitschr. f. Pilzk. 43: 145-173. 1977.
- BRIQUET, J., *International Rules of Botanical Nomenclature*. Jena, pp. I-XI, 1-152, 1935.
- BRODA, E., *The evolution of biogenetic processes*. - Pergamon Press. 1975.
- BRUCHET, G., *Contribution à l'étude du genre Hebeloma (Fr.) Kummer, partie speciale*. Bull. Soc. Linn. Lyon 39 suppl.: 1-132. 1970.
- BRUNEL, A., *Le metabolisme de l'azote purique chez les champignons*, p. 186. Paris 1936.
- BRUNSWICK, H., *Untersuchungen über die Geschlechts- und Kernverhältnisse bei der Hymenomycetengattung Coprinus*. - Bot. Abh. 5: 1-152. 1924.
- BUCHHOLTZ, F., *Beiträge zur Morphologie und Systematik der Hypogaeen*, pp. 1-196, pl. 1-5. Riga 1902.
- BULLER, R., *Researches on Fungi I-VI*. London 1909-34.
- BURGES, A., *Problems associated with the species problem in mycology*. - *Species studies in the British Flora* 1955: 65-82. 1955.
- BURLINGHAM, G.S., See under Murrill.
- CAPELLANO, A., *Position systématique du genre Macrocytidia*. - Bull. Soc. Myc. Fr. 92: 221-228. 1976.
- CEJP, K., *Revise středoeuropských druhů skupiny Mycena-Omphalia*. - Publ. Fac. Sc. Univ. Charles 98: 1-86. 1929; 100: 1-157. 1930.
- CHIU, WAI-FAN, *The Russulaceae of Yunnan*. - Lloydia 8: 31-59. 1945.
- CHOW, CHUNG WANG, *Contribution à l'étude du développement des Coprins*. - Le Botaniste 26: 89-210, pl. 9-20. 1934.
- CLÉMENÇON, H., *Die Metallbindungs-Vermögen der Lyophyllum-Granulation*. - Zeitschr. Pilzk. 36: 21-27. 1969.
- CLÉMENÇON, H., *Beiträge zur Kenntnis der Gattungen Lyophyllum Karsten und Calocybe Kühner I.* Zeitschr. Pilzk. 31: 29-35. 1966. II. Nova Hedwigia 14: 127-142. 1967.

- CLÉMENÇON, H., *Bemerkungen zum Nachweis der siderophilen Granulation der Lyophyllum-Basidie.* - Schweiz. Zeitschr. f. Pilzk. 46: 55-59. 1968.
- CLÉMENÇON, H., *Bau der Wände der Basidiosporen und ein Vorschlag zur Benennung ihrer Schichten.* Zeitschr. Pilzk. 36: 113-133. 1970.
- CLÉMENÇON, H., *Die Wandstruktur der Basidiosporen. II: Kuehneromyces mutabilis.* - Schweiz. Zeitschr. Pilzk. 50: 20-25. 1972. - III. *Cortinarius and Dermocyde.* - Zeitschr. f. Pilzk. 39: 121-144. 1973.
- CLÉMENÇON, H., *Die exkretorischen Cystiden von Baeospora myosura (Agaricales).* Zeitschr. f. Pilzk. 38: 55-71. 1972.
- CLÉMENÇON, H., *Die Phaeocystiden von Fayodia deusta (Agaricales).* Zeitschr. f. Pilzk. 38: 73-87. 1972.
- CLÉMENÇON, H., *Quantitative Schätzungen zur taxonomischen Stellung der Panaeoloideae.* - Zeitschr. f. Pilzk. 42: 45-56. 1976.
- CLÉMENÇON, H., (ed.) *The species concept in Hymenomycetes.* - Bibl. Mycol. 61: 1976.
- CLÉMENÇON, H., *Die Wandstrukturen der Basidiosporen VII.* - Zeitschr. f. Pilzk. 43: 283-289. 1977.
- CLÉMENÇON, H., *Siderophilous granules in the basidia of Hymenomycetes.* - Persoonia 10: 83-96. 1978.
- CLÉMENÇON, H., *Siderophilous granules in the basidia of Termitomyces.* - Mycol. Helvetica 1: 267-270. 1984. (publ. 1985).
- CONRAD, H.S., *The structure and development of Secotium agaricoides.* - Mycologia 7: 94-104. 1915.
- COKER, W.C., *The smaller species of Pleurotus in North Carolina.* - Journ. Elisha Mitchell Soc. 60: 73-95. 1944.
- COOKE, W.B., *The genera of Homobasidiomyceies*, 1-100. Beltsville 1951.
- COOKE, W.B., *The cyphellaceous fungi.* - Beih. Nov. Hedwigia 2: i-xv, 1-144, 1961.
- CORDA, A.J.C., *Icones fungorum hucusque cognitorum I-VI* (Vol. 6 edited by J.B. ZOBEL). 1838-54. (Reprint Lehre 1963.)
- CORNER, E.J.H., *An evolutionary study in Agarics.* - Trans. Brit. Myc. Soc. 19: 39-87. 1934.
- CORNER, E.J.H. *Hygrophorus with dimorphous basidiospores.* - Trans. Brit. Myc. Soc. 20: 157-184. 1936.
- CORNER, E.J.H., *Studies in the basidium.* - New Phytologist 47: 22-51. 1948.
- CORNER, E.J.H., *A monograph of Clavaria and allied genera*, i-xv, 1-740. London 1950.
- CORNER, E.J.H., *The construction of the polypores I. Introduction.* - Phytomorphology 3: 152-167. 1953.
- CORNER, E.J.H., *A monograph of cantharelloid fungi.* Oxford Univ. Press 255 pp. 1966.
- CORNER, E.J.H., *Phylloporus Quel. and Paxillus Fr. in Malaya and Borneo.* - Nov. Hedw. 20: 793-822. 1970.
- CORNER, E.J.H., *Meruliod fungi in Malaysia.* - Garden's Bull. Singapore 25: 355-381. 1971.
- CORNER, E.J.H., *Boletus in Malaysia.* Singapore 1972.
- CORNER, E.J.H., *The agaric genera Lentinus, Panus, and Pleurotus.* - Nov. Hedw. Beih. 69: 1-169. 1981.
- CRAWSHAY, R., *The spore ornamentation of the Russulas*, pp. 1-174, pl. 1-46. London. 1930.
- DANGEARD, P.A., *Mémoire sur la reproduction sexuelle des Basidiomycètes.* - Le Botaniste 4: 119-181. 1895.
- DEMOULIN, V., *Les Gasteromycètes.* - Les Naturalistes Belges. Bulletin 50: 225-270. 1969.

- DENNIS, R.W.G., *Some Agaricaceae of Trinidad and Venezuela, Leucosporae*, part. 1. - *Trans. Brit. Mycol. Soc.* 34: 411-482. 1951.
- DENNIS, R.W.G., *Lepiota and allied genera in Trinidad*, B.W.I. - *Kew Bull.* 1952: 459-500. 1952.
- DENNIS, R.W.G., *Pleurotoid fungi from the West Indies*. - *Kew Bull.* 1953: 31-46. 1953.
- DENNIS, R.W.G., *Some West Indian collections referred to Hygrophorus*. - *Kew Bull.* 1953: 253-268. 1953.
- DENNIS, R.W.G., *Les Agaricales de l'Ile de la Trinité: Rhodosporae-Ochrosporae*. - *Bull. Soc. Mycol. Fr.* 69: 145-198. 1953.
- DENNIS, R.W.G., *The fungus flora of Venezuela and adjacent countries*, pp. 1-531. London 1970.
- DENNIS, R.W.G., P.D. ORTON & F.B. HORA, *New Check List of British Agarics and Boleti*. - *Trans. Brit. Mycol. Soc.*, Supplement 1-225. 1960.
- DENNIS, R.W.G., & D.A. REID, *Some marasmoid fungi allegedly parasitic on leaves and twigs in the tropics*. - *Kew Bull.* 1957: 287-292. 1957.
- DOUGET, G., *Recherches sur le Rhodotus palmatus (Fr. ex Bull.) R. MAIRE*. - *Bull. Soc. Mycol. Fr.* 72: 61-87. 1956.
- DONK, M.A., *Revisie van de Nederlandse Heterobasidiomycetae en Homobasidiomycetae-Aphyllophoraceae*. - *Medd. Ned. Myc. Ver.* 18-20: 68-200. 1931.
- DONK, M.A., *Revision der niederländischen Homobasidiomycetae-Aphyllophoraceae II*. - *Medd. Bot. Mus. Herb. Utrecht* 9: 1-278. 1933.
- DONK, M.A., *The generic names proposed in Hymenomycetes-I. "Cyphellaceae"*. - *Reinwardtia* 1: 199-220. 1951.
- DONK, M.A., *The generic names proposed in Polyporaceae*. - *Persoonia* 1: 173-302. 1960.
- DONK, M.A., *Notes on "Cyphellaceae" I*. - *Persoonia* 1: 25-110. 1959. - II. 2: 331-348. 1962.
- DONK, M.A., *The generic names proposed for Agaricaceae*. - *Nova Hedwigia*. Suppl. Vol. 2, pp. 1-320. Weinheim/Bergstr. 1961.
- DONK, M.A., *A conspectus of the families of Aphyllophorales*. - *Persoonia* 3: 199-324. 1964.
- DONK, M.A., *Progress in the study of the classification of the Higher Basidiomycetes in PETERSEN, R., Evolution in the Higher Basidiomycetes*, Knoxville 1971, pp. 3-28.
- DONK, M.A., *Multiple convergence in the polyporaceous fungi in PETERSEN (1971)*, pp. 393-422.
- DÖRFELT, H., *Taxonomische Studien in der Gattung Xerula*. R. Mre. I-V. - *Fedde's Repertorium* 90: 363-388. 1979.; 91: 209-223. 1980; 415-438. 1980; 92: 255-291. 1981; 92: 631-674. 1981.
- DÖRFELT, H., *Die Fruchtkörperentwicklung von Xerula radicata*. - *Flora* 172: 533-561. 1982.
- DOUGLAS, G.E., *A study of development in the genus Cortinarius*. - *Amer. Journ. Bot.* 3: 319-335. 1916.
- DOUGLAS, G.E., *The development of some exogenous species of Agarics*. - *Amer. Journ. Bot.* 5: 36-54. 1918.
- DOUWES, G.A.C. & J.A. VON ARX, *Das hymenophorale Trama bei den Agaricales*. *Bot. Neerl.* 14: 197-217. 1965.
- DUNCAN, E.G. & M.H. GALBRAITH, *Post-meiotic events in the Homobasidiomycetidae*. *Trans. Brit. Mycol. Soc.* 58: 387-392. 1972.
- EDWARDS, B.L. & G.C. ELSWORTHY, *Variegatic acid...* *Chem. Commun.* p. 373-374. (Other important papers cited by Arpin & Kühner, 1977.)
- ELROD, R.P. & D.L. BLANCHARD, *Histological studies of the Boletaceae and related genera*. - *Mycologia* 31: 693-708. 1939.

- ELROD, R.P. & W.H. SNELL, *Development of the carpophores of certain Boletaceae*. - *Mycologia* 32: 493-504. 1940.
- EUGSTER, C.H., *Pilzfarbstoffe...* - *Zeitschr. f. Pilzk.* 39: 45-96. 1973.
- FARR, D.F., *The acanthocyte, a unique cell type in Stropharia (Agaricales)*. *Mycotaxon* 11: 241-249. 1980.
- FAVRE, J., *Les Dochmiopus de la region de Genève et Pleurotus chioneus*. - *Schweiz. Zeitschr. Pilzk.* 13: 145-150. 1935.
- FAVRE, J., *Champignons rares et peu connus des hauts-marais jurassiens*. - I. *Bull. Soc. Myc. Fr.* 52: 129-146. 1936; II. *ibid.* 53: 271-296. 1937.
- FAVRE, J., *Les champignons collybioides des cônes des essences résineuses*. - *Schweiz. Zeitschr. Pilzk.* 17: 162-168, 178-182. 1939.
- FAVRE, J., *Études mycologiques faites au Parc National Suisse (Ergebnisse der wissenschaftlichen Untersuchung des Schweizer Nationalparkes 11.)*, pp. 467-474, pl. I-II. 1945.
- FAVRE, J., *Les champignons supérieurs de la zone alpine du Parc National Suisse*. - *Res. Rech. scient. entrpr. Parc. Nat. suisse* 5: 1-212. 1955.
- FAVRE, J., *Catalogue descriptif des champignons supérieurs de la zone subalpine du Parc National Suisse*. - *Ibid.* 6: 323-610. 1960.
- FAYOD, V., *Hymenomycetes-Agaricinae in Schinz, Beiträge zur Kenntnis der Flora von Deutsch-Südwestafrika*. - *Verh. Bot. Ver. Brand* 31: 224-229. 1889.
- FAYOD, V., *Prodrome d'une histoire naturelle des Agaricinées*. - *Ann. Sc. Nat. Bot.* VII. 9: 181-411. 1889.
- FAYOD, V., *Vorläufige Bemerkung zur Frage des Autonomierechtes des Hymenoconidium petasatum*. - *Bot. Zeit.* 47: 158-159. 1889.
- FIASSON, J.L., *Les carotenoides des Basidiomycetes, survol chimotaxonomique*. Thèse, Lyon 1968.
- FIASSON, J.L., P. LEBRETON & N. ARPIN, *Les carotenoides des champignons*. *Bull. Soc. Nat. et Arch. Ain* 82: 47-67. 1968.
- FISCHER, C.C.E., *On the development of the fructification of Armillaria mucida*. - *Ann. Bot.* 23. 503-507. 1909.
- FISCHER, E., *Unterklasse Eubasidii. Reihe Gastromyctes* in ENGLER, A. & K. PRANTL, *Die natürlichen Pflanzenfamilien* 2nd. ed. Bd. 7a, i-iv, 1-122. 1933.
- FISCHER, E., *Neue Beiträge zur Kenntnis der Verwandtschaftsverhältnisse ...* - *Ber. Schweiz. Bot. Ges.* 45: 231-247. 1936.
- FITZPATRICK, H.M., *A comparative study of the fruit body in Phallogaster, Hysterangium and Gautiera*. - *Ann. Mycol.* 11: 119-149. 1913.
- FREREJACQUE, M., *Le mannitol chez les champignons*. - *Rev. Mycol.* 4: 89-100. 1939.
- FURTADO, J.S., *Significance of the clamp connections in the Basidiomycetes*. - *Persoonia* 4: 125-144. 1966.
- GABRIEL, M., *Recherches sur les pigments des Agaricales I*. *Ann. Un. Lyon* 10: 65-78. 1958. III. *Bull. Soc. Myc. Fr.* 76: 208-315. 1960. IV. *Ann. Un. Lyon* 11-12; 67-76, 1960. V. *Bull. Soc. Myc. Fr.* 77: 262-272. 1961. VI. *Ibid* 78: 359-366. 1962.
- GABRIEL, M., *Contribution à la Chimiotaxonomie des Agaricales*. Thèse, Lyon 1965.
- GAMS, H., *Die Halbflechten Botrydina und Coriscium als Basidiolichenen*. - *Österr. Bot. Zeitschr.* 109: 376-380. 1962.

- GARCIA, J. & J. CASTILLO, *Las especies de Boletaceos y Gomfidiaceos conocidas en Nuevo León.* - *Bol. Soc. Mex. Mic.* 15: 121-197. 1981.
- GAYLORD, M.C. & L.R. BRADY (1971) - Comparison of pigments in carpophores and saprophytic cultures of *Paxillus panuoides* and *Paxillus atrotomentosus*. In *J. Pharmac.* 60: 1503-1508.
- GENTILE, A.C. & W.H. SNELL, *Development of the carpophore of Boletinus paluster.* - *Mycologia* 45: 720-722. 1953.
- GERHARDT, E., *Über zwei neue Tricholomataceen.* *Zeitschr. f. Mykol.* 48: 239-243. 1982.
- GILBERT, E.J., *Le genre Amanita*, pp. 1-181. 1918.
- GILBERT, E.J., *Les Bolets*, pp. 1-225. Paris 1931.
- GILBERT, E.J., in Bresadola, *Iconographia Mycologica* 27(1-3), 1-417, pl. 1-73. Mediolani 1940-1.
- GILBERT, E.J., *Essai de terminologie des organes véliformes et annuliformes des Agaricales et Boletales.* - *Bull. Soc. Myc. Fr.* 63: 42-57. 1947.
- GILBERT, E.J. & R. KÜHNER, *Recherches sur les spores des Amanites.* - *Bull. Soc. Myc. Fr.* 44: 149-154. 1928.
- GILLIAM, M.S., *The genus Marasmius ...* - *Mycotaxon* 4: 1-144. 1976.
- X GLUCHOFF-FIASSON, K. & R. KÜHNER, *La délimitation et la classification des Strophariaceae à la lumière de nouvelles recherches sur la structure des pigments.* - *C.R. Acad. Sc., Paris* 284: 1667-1672. 1964.
- GODFRIN, J., *Caractères anatomiques des Agaricinés.* - *Bull. Soc. Sc. Nancy* III 1(6): 188-211. 1900 (1901).
- GRAND, L.F. & R.T. MOORE, *Ultracytotaxonomy of Basidiomycetes. I. Scanning electron microscopy of spores.* - *J. Elisha Mitchell Sci. Soc.* 86: 106-117. 1970.
- GRAY, S.F., *Natural arrangement of British plants.* 1: 1-824. 1821.
- GREIS, H., *Die Entstehung der Basidiomycetenschnallen aus den Ascomycetenhaken.* *Zeitschr. Wiss. Bot.* 86: 81-106. 1938.
- GRUBER, I., *Fluroeszierende Stoffe der Cortinarius-Untergattung Leprocyebe.* - *Zeitschr. Pilzk.* 35: 249-261. 1969.
- GRUBER, I., *Anthrachinonfarbstoffe in der Gattung Dermocybe und Versuch ihrer Auswertung für die Systematik.* - *Zeitschr. Pilzk.* 36: 95-112. 1970.
- GURWITSCH, A., *Über den Begriff des embryonalen Feldes.* - *Arch. Entwicklungsmechanik d. Organismen* 51: 383. 415. 1922.
- GUZMÁN, G., *The genus Psilocybe.* - *Nov. Hedw., Beih.* 74: 1-439, and illus. 1983.
- HALLING, R.E., *The genus Collybia (Agaricales) ...* - *Mycologia Mem.* 8, Cramer, Braunschweig, 1983.
- HANNA, W.F., *Notes on Clitocybe illudens.* - *Mycologia* 30: 379-384. 1938.
- HARMAJA, H., *The genus Clitocybe (Agaricales) in Fennoscandia.* - *Karstenia* 10: 1-121. 1969.
- HARMAJA, H., *On hygrophany of basidiocarp in the genus Clitocybe Kummer.* - *Karstenia* 9: 51-53. 1969.
- HARMAJA, H., *Type studies in Agaricales described as Clitocybe and Omphalina.* - *Karstenia* 11: 35-40. 1970.
- HEIKKILÄ, H. & P. KALLIO, *On the problem of subarctic Basidiolichens.* - *Ann. Univ. Turku A. II:* 36 (Rep. Kevo Subarct. Sta. 3) 48-74. 1966.
- HEIM, L., *Zur Sporenfärbung.* - *Ann. Mycol.* 36: 327-333. 1938.
- HEIM, R., *Sur les hyphes vasiformes des Agaricacés.* - *Compt. r. Acad. Sc.* 188: 1566. 1929.

- HEIM, R., *Les liens phylétiques entre les Agarics Ochrosporées et certains Gastromycètes*. - *C. r. Ac. Sc.* 192: 291. 1931.
- HEIM, R., *Le genre Inocybe*, pp. 1-419, pl. 1-35. Paris 1931.
- HEIM, R., *Champignons*, in *Mission Saharienne ... - Bull. du Muséum*, 2<sup>e</sup> sér. 4: 915-932, 3 pl., 1932.
- HEIM, R., *Fungi Iberici*. - *Treb. Mus. Ciènc. Nat. Barcelona* 15(3): 1-146, pl. 1-4. 1934.
- HEIM, R., *L'Olatafa*. - *Arch. Mus. Hist. Nat.* 12: 549-554. 1935.
- HEIM, R., *Les Volvaires*. - *Rev. Myc.* 1: Supplements 55-58, 85-90, 1936.
- HEIM, R., *Les Lactario-Russulés du domaine oriental de Madagascar*, pp. 1-196, Paris 1937 [1938].
- HEIM, R., *Les pigments des champignons*. - *Bull. Soc. Chim. Biol.* 29: 48-79. 1942.
- HEIM, R., *Remarques sur les formes primitives ou dégradées de Lactario-Russulés tropicaux*. - *Boissiera* 7: 266-280. 1943.
- HEIM, R., *Nouvelles études descriptives sur les Agarics termiteophiles d'Afrique tropicale*. - *Arch. Mus. Nat. Hist. Nat.* 18: 107-166. 1943.
- HEIM, R., *Un nouveau cas d'hétérosporisme chez les Inocybes*. - *Rev. Mycol.* 8: 32-49. 1943.
- HEIM, R., *Observation sur la flore mycologique Malgache*. - III. *Rev. Mycol.* 1: 3-18, pl. 1-4. 1936; IV. *Rev. Mycol.* 1: 223-256. 1936; V. *Rev. Mycol.* 2: 4-17, 61-75, 1937; VI. *Boletim Soc. Broteriana* 13: 45-3, pl. I-II, 1938; VII. *Rev. Mycol.* 4: 5-20, 1939; VIII. *Les Agarics tropicaux à hymenium tubulé*. *Rev. Mycol.* 10: 3-61, pl. 1-4. 1945 [1946].
- HEIM, R., *Les Sympodiae ou Marasmes arborescents du Cameroun*. - *Ann. Sc. Nat. Bot.* 9: 1-8. 1948.
- HEIM, R., *Note sur la flore mycologique des Terres du Pacifique Sud*. II. *Cuphocyste*, nouveau genre néo-zélandais d'Agarics ochrosporés. - *Rév. d. Mycol.* 16: 3-10. 1951.
- HEIM, R., *Les Termitomyces du Cameroun et du Congo français*. - *Mém. Soc. Helv. Sc. Nat.* 80(1): 1-29. 1952.
- HEIM, R., *Les Lactaires d'Afrique intertropicale*. - *Bull. Jard. Bot. État* 25: 1-91. 1955.
- HEIM, R., *Nouvelles contributions à la flore mycologique mexicaine*. - *Rev. d. Mycol.* 24: 185-196. 1959.
- HEIM, R., *Les champignons associés à la folie des Kuma*. - *Cahiers du Pacifique* 7: 7-64. 1965.
- HEIM, R., *L'imbroglio du Boletus leptopus*. - *Rev. Myc.* 31: 400-404. 1967.
- HEIM, R., *Anomalies hymeniales chez un Hygrophore*. - *Rev. Myc.* 23: 291-296. 1969.
- HEIM, R., *Particularités remarquables des Russules tropicales "Pelliculariae" lilliputtiennes - les complexes annulata et radicans*. - *Bull. Soc. Myc. Fr.* 86: 59-77. 1970.
- HEIM, R., *Les Meiorganés. phylum reliant les bolets aux polypores*. - *Rev. Mycol.* 30: 307-339. 1966.
- HEIM, R., *The interrelationships between the Agaricales and Gasteromycetes* in R.H. Petersen (1971b), pp. 505-534.
- HEIM, R., A. BRACK, H. KOBEL, A. HOFMANN & R. CAILLEUX, *Determinism de la formation des carpophores et des sclérotes dans la culture du Psilocybe mexicana*. - *C.R. Acad. Science.* 246: 1346-1351. 1958.
- HEIM, R. & R.G. WASSON, *Les champignons hallucinogènes du Mexique*. - *Arch. Mus. Nat. Hist. Nati.* 7 sér. 6. IV-VIII: 279-318. 1958 (publ. Febr. 1959).
- HEINEMANN, P., *Champignons recoltés au Congo Belge par Madame M. Goossens-Fontana*. - I. *Boletineae*. - *Bull. Jard. Bot. État* 21: 223-346. 1951 - II. *Agaricus Fr. s.s.* - *Ibid.* 26: 1-136. 1956. - V. *Hygrophoraceae*. - *Ibid.* 33: 421-458. 1963.
- HEINEMANN, P., *Les Boletinées*. - *Les Naturalistes Belges*, *Bull.* 42: 333-362. 1961.
- HEINEMANN, P., *Les critères systématiques chez les Cantharellineae*. - *Sydowia* 15: 200-203. 1961.

- HEINEMANN, P., *Leucoprineae p.p. in Flore illustrée champ. d'Afrique Centrale* 2. 1973.
- HEINEMANN, P., *The genus Micropsalliotia*. - *Kew Bull.* 31: 581-583. 1976.
- HEINEMANN, P., *Leucocoprinus in Flora illustrée champ. d'Afrique Centrale* 5. 1977
- HEINEMANN, P., *Leucocoprines nouvelles d'Afrique centrale*. - *Bull. Jard. Bot. Nat. Belg.* 47: 83-86. 1977.
- HEINEMANN, P., *Sericeomyces, genre nouveau de Leucocoprineae (Agaricaceae)*. - *Bull. Jard. Bot. Nat. Belg.* 48: 399-407. 1978.
- HEINEMANN, P., *Les genres Agaricus et Micropsalliotia en Malaisie et en Indonésie*. - *Bull. Jard. Bot. Nat. Belg.* 50: 3-68. 1980.
- HEINEMANN, P. & J. CASIMIR, *Distribution des acides aminés libre dans le genre Agaricus (Psalliotina)*. - *Rev. Myc.* 26: 24-33. 1961.
- HEINEMANN, P. & J. RAMMELOO, *Observations sur Gyroporus castaneus s.l.* - *Bull. Jard. Bot. Nat. Belg.* 49: 435-447. 1979.
- HEINEMANN, P. & J. RAMMELOO, *Observations sur le genre Phlebopus*. - *Mycotaxon* 15: 384-404. 1982.
- HEINEMANN, P. & D. THOEN, *Observations sur le genre Cystoderma*. - *Bull. Soc. Myc. Fr.* 89: 5-35. 1973.
- HENRY, R., *Réactions colorées obtenues sur les champignons supérieurs à l'aide d'un réactif de synthèse*. - *Rev. Mycol.* 8: 22-25. 1943.
- HERINK, J., *Stavnatkovité Houby pahorku "Velka Horka" u Mnichova Hradisté*. - *Acta Mus. Bot. sept. Liberecensis* 1: 53-86. 1959.
- HERINK, J., F. KOTLABA & Z. POUZAR, *Limkovka ocesaná - Stropharia hornemannii (Fr. ex Fr.) Lund. & Nannf.* - v Československu. - *Česk. Mikologie* 11: 13-20. 1957.
- HERVEY, A.C.T. BOGERSON & I. LEONG, *Studies on fungi cultivated by ants* - *Brittonia* 29: 226-236. 1977.
- HESLER, L.R., *North American species of Gymnopilus*. - *Mycologia Memoir* 3: 1-117. 1969.
- HESLER, L.R. & A.H. SMITH, *North American species of Hygrophorus*. i-vii, 1-416. 1963.
- HESLER, L.R. & A.H. SMITH, *North American species of Crepidotus*, pp. 1-168. 1965.
- HESLER, L.R. & A.H. SMITH, *North American species of Lactarius*. - *Ann Arbor* 1979.
- HILBER, O., *Die Gattung Pleurotus (Fr.) Kummer*. Cramer, Vaduz, 1982.
- HINTIKKA, E.V.K., *Über die finnischen Arten und Varietäten der Gattung Xeromphalina Kühner & Maire*. - *Karstenia* 4: 5-9. 1957.
- HIROFUMI, TERAKAWA, *Studies on the morphogenesis in Pleurotus ostreatus*. - *Sc. Pap. Coll. Gen. Educ. Univ. Tokyo* 6(1): 61-87. 1956.
- HOFFMANN, H., *Beiträge zur Entwicklungsgeschichte und Anatomie der Agaricineen*. - *Bot. Zeitung* 18: 389-397, pl. 1860.
- HOFFMANN, H., *Icones analyticae fungorum I-IV*. 105 pp., pl. 1-24. Gießen 1861-5.
- HOLLAND, A.A. & D.N. PEGLER, *Hebeloma victoriense and the genus Metraria*. - *Trans. Brit. Myc. Soc.* 80: 157-186. 1983.
- HOLTERMANN, C., *Mykologische Untersuchungen aus den Tropen*, i-viii. 1-122. 1898.
- HONGO, TSUGUO, *The Agaricales of Japan*. - *Mem. Fac. Lib. Arts Shiga Un.* 9: 47-94; 10: 61-72. 1959-60. *Act. Phyt.* 18: 129-146. 1960.
- HONGO, TSUGUO, *Notes on Japanese fungi*. - *J. Jap. Bot.* 42: 151-159. 1967.

- HORA, F.B., *New Check List of British Agarics and Boleti*, part 4. - *Trans. Brit. Mycol. Soc.* 43: 440-459. 1960.
- HORAK, E., *Synopsis generum Agaricalium*. - *Beitr. Krypt.-fl. Schweiz* 13: 1-741. 1968.
- HORAK, E., *Studies on the genus Descolea Sing.* - *Persoonia* 6: 231-248. 1971.
- HORAK, E., *Contributions to the knowledge of the Agaricales s.l. (Fungi) of New Zealand*. *N.Z.J. Bot.* 9: 463-493. 1971.
- HORAK, E., *A contribution towards the revision of the Agaricales (Fungi) of New Zealand*. *New Zeal. J. Bot.* 9: 403-462. 1971.
- HORAK, E., *Crepidotus episphaeria and related species from the Southern Hemisphere*. *Ber. Schweiz. Bot. Ges.* 87: 227-235. 1977.
- HORAK, E., *Paxilloid Agaricales in Australasia*. - *Sydowia* 32: 154-166.
- HORAK, E., *in Flora cryptogamica de Tierra de Fuego; orden Agaricales*. (Guarrera, Gamundi de Amos & Rabinovich de Halperin, dir.) 11: 1-524. 1979.
- HORAK, E., *Taxonomy and distribution of two little known monotypic genera of Agaricales; Amparoina, Cystoagaricus*. - *Sydowia* 33: 64-70. 1980.
- HORAK, E., *Neufunde und Bemerkungen zu einem emendierten Gattungskonzept von Pterospora Metrod (Agaricales)*. - *Sydowia* 36: 125-138. 1983.
- HORAK, E., *Mycogeography in the South Pacific region: Agaricales, Boletales*. - *Austr. Journ. Bot., Suppl. Ser.* 10: 1-41. 1983.
- HUIJSMAN, H.S.C., *Opmerkingen en problemen betreffende de taxonomie van het geslacht Amanita*. - *Med. Ned. Myc. Ver.* 26: 1-27. 1942.
- HUIJSMAN, H.S.C., *Observations sur le "genre" Lepiota*. - *Ibid.* 28: 3-60. 1943.
- HUIJSMAN, H.S.C., *Hebelomina microspora, nov. spec.* - *Rev. d. Mycol.* 11: 31-33. 1946.
- HUIJSMAN, H.S.C., *Quelques champignons rares*. - *Bull. Soc. Nat. Oyonnax* 7: 69-79. 1953.
- HUIJSMAN, H.S.C., *Cotylidia carpatica (Pilat) comb. nov.* - *Bull. Soc. Mycol. Fr.* 70: 57-62. 1954.
- HUIJSMAN, H.S.C., *Observations on agarics*. - *Fungus* 25: 18-43. 1955.
- HUIJSMAN, H.S.C., *Three remarkable white-spored agarics collected in Switzerland*. - *Fungus* 26: 38-43. 1956.
- HUIJSMAN, H.S.C., *Sur quatre Strophariaceae*. - *Fungus* 27: 43-49. 1957.
- HUIJSMAN, H.S.C., *Note complémentaire à propos de Cystoderma superbum Huijsm.* - *Fungus* 28: 47. 1958.
- HUIJSMAN, H.S.C., *Deux Amanites méconnues*. - *Bull. Soc. Mycol. Fr.* 75: 14-32. 1959.
- HUIJSMAN, H.S.C., *Note sur le genre Agaricus*. - *Observations sur les Lepioteae Fayod - Mycena minor Huijsm., spec. nov. et Mycena pseudopicta (J. Lange) Kühn.* - *Observations sur le genre Ripartites*. - *Persoonia* 1: 321-339. 1960.
- HUIJSMAN, H.S.C., *Observations sur le genre Hohenbuehelia*. - *Persoonia* 2: 101-107. 1961.
- HUMBLOT, R., *Notes sur deux espèces américaines ...* - *Bull. Soc. Mycol. Fr.* 42: 75-80. 1926.
- IMAI, SANSHI, *Studies of the Agaricaceae of Hokkaido I, II*. - *Journ. Fac. Agron. Hokkaido Imp. Univ.* 43: 1-378. 1938.
- IMAZEKI, ROKUYA, *The Boletaceae of Japan*. - *Nagaoa* 2: 30-46. 1952.
- IMAZEKI, ROKUYA & TSUGUO HONGO, *Coloured Illustrations of Fungi of Japan I-VIII*. 1-181, 68 plts. Hoikusa, Okasa 1957.
- ITO, S., *Mycological Flora of Japan 2 (no. 5), Agaricales, Gasteromycetales*, 1-658, Tokyo 1959.

IWADE, I., *Studies of Japanese fungi*. - Bull. Imp. Univ. For. 33: 51-64. 1944.

JACKSON, H.S., *Life cycles and phylogeny in the higher fungi*. - Trans. Roy. Soc. Can. III (5) 38: 1-32. 1944.

JACQUES-FELIX, M., *Recherches morphologiques, anatomiques, morphogénétiques et physiologiques sur le rhizomorphe des champignons supérieurs et sur le déterminisme de leur formation*. - Bull. Soc. Myc. Fr. 84: 161-307. 1968.

JAHRMANN, H.J. & W. PRILLINGER, *Das Vorkommen eines "Hefe"-Stadiums bei dem Homobasidiomyzeten Asterophora (Nyctalis) lycoperdoidea*. - Zeitschr. f. Mykologie 49: 195-226. 1983.

JOSSERAND, M., *Un nouveau champignon producteur d'acide cyanhydrique*. - Bull. Soc. Linn. Lyon 1: 1-4. 1932.

JOSSERAND, M., *Sur la nature de la trame dans les genres Paxillus et Phylloporus*. - Bull. Soc. Myc. Fr. 48: 112-117, pl. 13. 1932.

JOSSERAND, M., *Importance de l'ornementation piléique pour la détermination des Coprins. L'étude des Coprins simicoles*. - Ann. Soc. Linn. Lyon 77: 1-27. 1944.

JOSSERAND, M., *Description d'une Collybie exotique ...* - Bull. Soc. Myc. Fr. 51: 243-248. 1935.

JOSSERAND, M., *Description de quelques Omphales blanches*. - Ann. Soc. Linn. Lyon 80: 1-20. 1936.

JOSSERAND, M., *Sur les dimorphismes des cheilocystides*. - Bull. Soc. Myc. Fr. 52: 102-110. 1936.

JOSSERAND, M., *Remarques sur la valeur taxonomique de la bisporicité chez les champignons supérieurs*. Bull. Soc. Linn. Lyon 6: 1-3. 1937.

JOSSERAND, M., *Deux nouvelles Agaricacées dégageant de l'acide cyanhydrique*. - Rev. Mycol. 3: 29-30. 1938.

JOSSERAND, M., *Étude sur les espèces françaises du genre Clitopilus*. - Bull. Soc. Linn. Lyon 10: [1]-[15]. 1941.

JOSSERAND, M., *Étude sur l'ornementation sporique des Lactaires et de quelques autres espèces à spores amyloïdes*. - Bull. Soc. Myc. Fr. 56: 7-38, pl. 1-12. 1941.

JOSSERAND, M., *Notes critiques sur quelques champignons de la région Lyonnaise*. - I. Bull. Soc. Myc. Fr. 49: 340-376. 1933; II. ibid. 53: 175-230, pl. 6. 1937; III. ibid. 49: 5-34. 1943; IV. ibid. 64: 3-30. 1948; V. ibid. 71: 65-125. 1955.

JOSSERAND, M., *Une espèce nouvelle de Tricholomée: Tricholoma (Dermoloma) Hygrophorus*. - Bull. Soc. Myc. Fr. 74: 482-491. 1958.

JOSSERAND, M., *La description des champignons supérieurs*. - Encycl. Mycol. 21: 1-338. 1952.

JOSSERAND, M. & P. KONRAD, *Notes sur deux Collybia de group clusilis*. - Bull. Soc. Linn. Lyon 10: 19-23. 1931.

JOSSERAND, M. & R. KÜHNER, *Un Marasme peu commun: Marasmius torquescens Q.* - Bull. Soc. Myc. Fr. 49: 218-224. 1933.

JOSSERAND, M. & R. MAIRE, *Sur l'Omphalia marginella (Pers.) Joss. et Maire*. - Bull. Soc. Linn. Lyon 10: 115-119. 1931.

JOSSERAND, M. & G. NÉTIEN, *Observations sur la fluorescence ...* - Bull. mens. Soc. Linn. Lyon 1938(10): 238-292. 1939 (1): 14-23. 1938-9.

JOSSERAND, M. & A. POUCHET, *Note sur une Agaricacée tchécoslovaque récoltée dans la région Lyonnaise: Collybia rhizophora Velen.* - Bull. Soc. Linn. Lyon 10: 51-54. 1931.

JUEL, H.O., *Die Kernteilung in den Basidien und die Phylogenie der Basidiomyceten*. - Jahrb. Wiss. Bot. 32: 361-388. 1898.

JUEL, H.O., *Cytologische Pilzstudien. I. - Nov. Acta R. Soc. Sc. Upps. IV. 4(6): 1-40*. 1916.

JÜLICH, W., *Higher taxa of Basidiomycetes*. - Bibliotheca Mycologica 85. Cramer, Vaduz, 1981.

KALAMÈES, K., *K sistematike i rasprostraneniyu vidov Strobilurus i Baeospora v Estonii. Trans. Tartu State Univ.* 268: 373-404. 1970.

KALLENBACH, F., *Die Röhrlinge. - Die Pilze Mitteleuropas I.* - 1-158. 1926-38.

KÄMMERER, A., H. BESL & A. BRESINSKY, *Omphalotaceae fam. nov. and Paxillaceae. - Syst. & Evol.* 150: 101-117. 1985.

KAUFFMAN, C.H. (see Murrill).

KELLER, J., *Ultrastructure de la paroi sporique de Pachykytospora et de Gomphus. - Ber. Schweiz. Bot. Ges.*, in press.

KELLER, J., *Ultrastructure de la paroi sporale de Heterobasidion annosum. - Schweiz. Zeitschr. Pilzk.* 86: 97-99. 1973.

KNIEP, H., *Über das Auftreten von Basidien im einkernigen Myzel von Armillaria mellea. Fl. Dan. - Zeitschr. Bot.* 3: 529-553. 1911.

KNIEP, H., *Die Sexualität der niederen Pflanzen*, 544 pp. Jena 1928.

KÖGL & al. *Untersuchungen über Pilzfarbstoffe I-IX. - Liebig's Ann. Chem.* 440: 19-35; 465: 211-242; 482: 105-119. 1924-1930.

KONRAD, P., *Les Lactaires. - Bull. Soc. Myc. Fr.* 51: 160-191. 1935.

KONRAD, P. & A. MAUBLANC, *Icones selectae fungorum.* 1-5: pl. 1-500; 6: I-XVI, 1-558. 1924-36 [1937].

KONRAD, P., *Les Agaricales. - Encyclopédie Mycologique*, 14 & 20: 1-469 & 1-182. 1948-52.

KORHONEN, K., *Interfertility and clonal size in the Armillariella mellea complex. - Karstenia* 18: 31-42. 1978.

KORHONEN, K., *The origin of clamped and clampless basidia in Armillariella octoyae. - Karstenia* 20: 23-27. 1980.

KORHONEN K. & V. HINTIKKA, *Cytological evidence for somatic diploidization in dicaryotic cells of Armillariella mellea. - Arch. Microbiol.* 95: 187-192. 1974.

KOTLABA, F., *Bemerkungen zur Auffassung der Gattung bei den Makromyzeten. - Preslia* 36: 329-336. 1964.

KOTLABA, F. & Z. POUZAR, *Preliminary results of the staining of spores ... in cotton blue ... - Fedde's Rep.* 69: 131-142. 1964.

KREISEL, H., *El papel de los hongos en la vegetación forestal de Cuba. - Bol. Soc. Mex. Mic.* 4: 39-43. 1970.

KREISEL, H., *Grundzüge eines natürlichen Systems der Pilze.* 245 pp. Lehre 1968.

KREISEL, H., *Ektotrophe Mykorrhiza bei Coccoloba uvifera in Kuba. - Biol. Rundschau* 9: 97-98. 1971.

KÜHNER, R., *Sur la nature des cystides chez les Basidiomycètes. - Compt. r. Acad. Sc.* 180: 454. 1925.

KÜHNER, R., *Le development de Lentinus tigrinus. - Bull. C. R. Ac. Sc.* 180, p. 137, 1925.

KÜHNER, R., *Contribution à l'étude des Hyménomycètes et spécialement des Agaricacées. - Le Botaniste* 17: 5-218. 1926.

KÜHNER, R., *Remarques sur les genres Lepista et Leucopaxillus. - Bull. Soc. Linn. Lyon* 5: 125-126. 1926.

KÜHNER, R., *Le développement du Boletinus cavipes (Opat.) Kalchbr. - Le Botaniste*, série 18: 9-13, pl. 6-7. 1927.

KÜHNER, R., *Le développement et la position taxonomique de l'Agaricus disseminatus Pers. - Le Botaniste*, série 20: 147-156. 1928.

KÜHNER, R., *Notes sur Lentinus variabilis Schulz. - Bull. Soc. Myc. Fr.* 44: 331-335. 1928.

- KÜHNER, R., *Note sur le Leucopaxillus amarus (Fries) mihi*. - Ann. Soc. Linn. 73: 1-3. 1928.
- KÜHNER, R., *Utilisation de l'acide sulfurique comme réactif du pigment sporique dans la systématique des Agarics mélanosporés*. - Bull. Soc. Linn. Lyon 8: 89. 1929.
- KÜHNER, R., *La position taxonomique de l'Agaricus separatus Linné*. - Bull. Soc. Linn. Lyon 8: 112. 1929.
- KÜHNER, R., *Description de quelques espèces nouvelles de Naucoria du groupe Alnicola*. - Bull. Soc. Mycol. Fr. 47: 237-243. 1931.
- KÜHNER, R., *Études sur le genre Marasmius*. - Le Botaniste 25: 57-116, pl. 5-7. 1933.
- KÜHNER, R., *A propos du genre Melanophyllum*. - Bull. Soc. Linn. Lyon 2: 75-77. 1933.
- KÜHNER, R., *Observations sur la localisation cytologique des substances colorées chez les Agarics et le Bolets*. - Le Botaniste 26: 347-370. 1934.
- KÜHNER, R., *Utilisation du bleu de crésyl en mycologie systématique*. - C. r. Acad. Sc. 198: (1)-(3). 1934.
- KÜHNER, R., *Deux espèces rares d'Agarics à revêtement piléique celluleux*. - Bull. Soc. Linn. Lyon 4: 50-51. 1935.
- KÜHNER, R., *Recherches sur le genre Lepiota*. - Bull. Soc. Myc. Fr. 52: 175-238. 1936.
- KÜHNER, R., *Observations sur le genre Hypoloma*. - Bull. Soc. Myc. Fr. 52: 9-30. 1936.
- KÜHNER, R., *Nouvelles recherches sur le genre Marasmius*. - Ann. Soc. Linn. Lyon 79: 1-22. 1936.
- KÜHNER, R., *Quelques mots sur la classification des Agarics ianthinosporés et melanospores*. - Bull. Soc. Myc. Fr. 52: 31-34. 1936.
- KÜHNER, R., *Utilisation du carmin acétique dans la classification des Agarics leucosporés*. - Bull. Soc. Linn. Lyon 7: 204. 1938.
- KÜHNER, R., *Le genre Mycena (Fries)*, pp. 1-710. Paris 1938.
- KÜHNER, R., *Observations taxonomiques et cytologiques sur quelques Naucoria du groupe Alnicola*. - Ann. Univ. Lyon. 3<sup>e</sup> ser. Science Nat. 1-15. 1942.
- KÜHNER, R., *Les Omphales bisporiques ou sans boucles*. - Bull. Soc. Linn. Lyon 12: 151-156. 1943.
- KÜHNER, R., *Nouvelles recherches sur les divisions nucléaires dans la baside et les spores des Agaricales*. - C. r. Acad. Sc. 220: 618-620. 1945.
- KÜHNER, R., *Le problème de la filiation des Agaricales à la lumière de nouvelles observations d'ordre cytologique sur les Agaricales leucosporées*. - Bull. Soc. Linn. Lyon 14: 160-166. 1945.
- KÜHNER, R., *Agaricus (Clitocybe) hirneolus Fries*. - Bull. Soc. Myc. Fr. 62: 1-11. 1946.
- KÜHNER, R., *Recherches morphologiques et caryologiques sur le mycélium de quelques Agaricales en culture pure*. - Bull. Soc. Mycol. Fr. 62: 1-48. 1946.
- KÜHNER, R., *Étude morphologique et caryologique du mycélium et des formations mycéliennes du Flammula gummosa (Lasch)*. - Rev. d. Mycol. 11: 3-30. 1946.
- KÜHNER, R., *Place de Bolets ... - Soc. Naturalistes d'Oyonnax*, Bull. no. 2: 37-48. 1948.
- KÜHNER, R., *Remarques sur quelques caractères microscopiques habituellement négligés des Cortinaires ... - Bull. Soc. Nat. Oyonnax* 3: 1-8. 1949.
- KÜHNER, R., *Le comportement nucléaire dans les articles du stipe des Agarics et des Bolets*. - Ann. Un. Lyon, sect. C. 10, 5-20. 1958.
- KÜHNER, R., in H. CLEMENÇON (ed.). *The species concept in Hymenomycetes*, pp. 157-187; 409-439, 8 pts. 1977.
- KÜHNER, R., *Vers un système phylogénétique des Camarophyllus et des Hygrocybe*. - Rev. Myc. 41: 73-90. 1977.

- KÜHNER, R., *Les grandes lignes de la classification des Agaricales, Asterosporales et Boletales. Survey historique et critique*. Bull. Soc. Linn. Lyon 46: 81-82. 1977.
- KÜHNER, R., *Les grandes lignes de la classification des Agaricales. Pluteales. Tricholomatales*. Bull. Soc. Linn. Lyon 47-49. 1978-1980.
- KÜHNER, R., *Some mainlines of classification in the gill fungi*. - Mycologia 76: 1059-1074. 1984.
- KÜHNER, R. & J. BOURSIER, *La forme des spores chez les Agarics Rhodogoniosporés*. - Bull. Soc. Myc. Fr. 45: 264-277. 1929 [1930].
- KÜHNER, R. & S. BOURSIER, *Notes sur le genre Inocybe*. - Bull. Soc. Mycol. Fr. 48: 118-341. 1932.
- KÜHNER, R. & R. MAIRE, *Étude de la réaction de la membrane sporique à l'oïde dans les divers genres d'Agarics leucosporés*. - Bull. Soc. Mycol. Fr. 50: 9-24. 1934.
- KÜHNER, R. & H. ROMAGNESI, *Flore analytique des champignons supérieurs (Agarics, Bolets, Chantarelles)*, i-xiv, 1-556. Masson & Cie, Paris 1953.
- KÜHNER, R. & H. ROMAGNESI, *Compléments à la Flore analytique III*. - Bull. Soc. Nat. Oyonnax 8: 73-131. 1954.
- KÜHNER, R., H. ROMAGNESI & H.C. YEN, *Définitions morphologiques entre plusieurs souches de Coprins de la section Micacei et confrontation de leurs haplotypes*. - Bull. Soc. Mycol. Fr. 63: 169-186. 1947.
- KÜHNER, R. & R. VANDENDRIES, *Un nouvel Agaric homothallique*. - Revue d. Cytologie et Cytophysiologie Vég. 2: 221-228. 1937.
- KÜRNSTEINER, H. & M. MOSER, *Isolation of a lethal toxin from Cortinarius orellanus Fr.* - Mycopathologia 74: 65-72. 1981.
- LAMOURE, D., *Recherches cytologiques et expérimentales sur l'amphithallie et la parthenogénèse chez les Agaricales*. - Thèse, 114, pp. 1960.
- LAMOURE, D., *Evolution nucléaire dans la baside des formes parthenogénétiques tetrasporiques de 3 espèces d'Omphalina (Agaricales)*. - Bull. Soc. Myc. Fr. 85: 247-249. 1969.
- LAMOURE, D., *Agaricales de la zone alpine. Rhodocybe borealis Lange & Skifte et sa position systématique*. - Svensk Bot. Tidskr. 65: 278-282. 1971.
- LAMOURE, D., *Agaricales de la zone alpine. Genre Clitocybe*. - Trav. Sc. Parc Nat. d.l. Vanoise 2: 107-152. 1972.
- LAMOURE, D., *Agaricales de la zone alpine. Genre Omphalina*. - Trav. Sci. Parc. Nat. Vanoise 5: 149-164. 1974.
- LANGE, J.E., *Studies in the Agarics of Denmark*. - I. Dansk. Bot. Ark. 1 (5). 1914; II. ibid. 2 (3). 1915; III. ibid. 2 (7). 1917; IV. ibid. 2(11). 1921; V. ibid. 4(4). 1923; VI. ibid. 4 (12). 1926; VII. ibid. 5(5). 1928; VIII. ibid. 6(5). 1930; IX. ibid. 8(3). 1933; X. ibid. 8(7). 1935; XI. ibid. 9(1). 1936; XII. ibid. 9(6). 1938.
- LANGE, J.E., *Flora Agaricina Danica I-V*. - Copenhagen 1935-40.
- LANGE, M., *Species concept in the genus Coprinus*. - Dansk. Bot. Ark. 14(6): 1-164. 1952.
- LANGE, M., *Macromycetes II. Greenland Agaricales*. - Medd. Gronland 147 (11): 1-70. 1955.
- LANGE, M., *Macromycetes III*. - Ibid. 148 (2): 1-125. 1957.
- LANGE, M. & L. HANSEN, *The phylogenetic position of the Agaricales*. - Bot. Tidskr. 51: 185-194. 1954.
- LARGENT, D.L. & R.G. BENEDICT, *Studies on the rhodophylloid fungi I. Generic concepts*. - Madoño 21: 32-39. 1971.
- LARGENT, D.L. & R.G. *Studies on the rhodophylloid fungi II. Alboleptonia, a new genus*. - Mycologia 62: 437-452. 1970.
- LARGENT, D.L. & R.G. BENEDICT, *The genus Leptonia ... Bibl. Mycol. 55*. Cramer, Vaduz, 1977.

- LENNOX, J.W., *Collybioid genera in the Pacific Northwest*. - *Mycotaxon* 9: 117-231. 1979.
- LENTZ, P.L., *Analysis of modified hyphae as a tool in taxonomic research in the Higher Basidiomycetes* in PETERSEN (1971b).
- LEVINE, M., *Studies in the cytology of Hymenomycetes*. - *Bull. Torr. Bot. Cl.* 40: 137-181. 1913.
- LEVINE, M., *The origin and development of the lamellae in Coprinus micaceus*. - *Amer. Journ. Bot.* 1: 343-356. 1914.
- LEVINE, M., *The origin and development of the lamellae in Agaricus campestris and in certain species of Coprinus*. - *Amer. Journ. Bot.* 9: 509-533. 1922.
- LINDER, D.H., *The genus Schizophyllum*. I. *The species of the western hemisphere*. - *Amer. Journ. Bot.* 20: 552-564. 1933.
- LOCQUIN, M., *Nouvelle technique d'étude des périspores amyloïdes; application au développement des spores de Fayodia bisphaerigera (Lange)* Kühner. - *Bull. Soc. Linn. Lyon* 12: 110-112, 122-128. 1943.
- LOCQUIN, M., - *Étude de développement des spores du genre Leucocoprinus Pat.* - *Bull. Soc. Linn. Lyon* 11: 39-48. 1942; 12: 35 seq., 91 seq. 1943.
- LOCQUIN, M., *La disposition des micelles calloso-pectiques dans les membranes des spores de quelques Basidiomycètes*. - *Bull. Soc. Myc. Fr.* 59: 44-51. 1943.
- LOCQUIN, M., *Sur le polymorphism de Clitopilus omphaliformis Joss.* - *Bull. Soc. Linn. Lyon* 13: 107-108. 1944.
- LOCQUIN, M., *Les divers modes de déhiscence périsporiique; leur répartition systématique chez les Agaricales*. - *Bull. Soc. Linn. Lyon* 13: 123-127. 1944.
- LOCQUIN, M., *Le développement des spirales gauches à la surface des spores de Laccaria et quelques remarques qu'il suggère*. - *Bull. Soc. Linn. Lyon* 14: 41-43. 1945.
- LOCQUIN, M., *Morphologie et structure des spores de Russula*. - *Rev. d. Mycol.* 13: 10-29. 1948.
- LOCQUIN, M., *Sur la non-validité de quelques genres d'Agaricales*. - *Bull. Soc. Mycol. Fr.* 68: 165-169. 1952.
- LOCQUIN, M., *Nouveau réactif pour l'étude des structures membranaires fines chez les champignons*. - *Bull. Soc. Mycol. Fr.* 68: 172-174. 1952.
- LOCQUIN, M., *Les colorations et les pigments chez les champignons supérieurs*. - *Bull. Soc. Mycol. Fr.* 69: 326-331. 1953.
- LOHWAG, H., *Entwicklungsgeschichte und systematische Stellung von Secotium agaricoides*. - *Oesterr. Bot. Zeit.* 73: 161-174. 1924.
- LOHWAG, H., *Zur Stellung und Systematik der Gastromyceten*. - *Verh. Zool. Bot. Ges.* 74: 38-55. 1924.
- LOHWAG, H., *Die Homologie im Fruchtkörperbau der höheren Pilze*. - *Biologia Generalis* 2: 148-181, 575-608. 1926.
- LOHWAG, H., *Zur Entwicklungsgeschichte und Morphologie der Gastromyceten*. - *Beih. Bot. Centralbl.* 42(22): 174-334. 1926.
- LOHWAG, H., *Zur Kenntnis der Manschette von Amanita*. - *Ann. Mycol.* 31: 126-133. 1926.
- LOHWAG, H., *Mykologische Studien X*. - *Biologia Generalis* 10: 457-468. 1934.
- LOHWAG, H., *Bulbillose bei Blätterpilzen*. - *Österr. Bot. Zeitschr.* 85: 65-68. 1936.
- LOHWAG, H., in H. HANDEL-MAZZETTI, *Symbolae Sinicae II. - Fungi*, pp. 37-66. 1937.
- LOHWAG, H. *Anatomie der Asco- und Basidiomyceten*. - *Handbuch der Pflanzenanatomie* 6(II, 3). 1941.
- LOHWAG, H. & M. PERINGER, *Zur Anatomie der Boletaceae*. - *Ann. Mycol.* 35: 295-331. 1937.

- MAAS GEESTERANUS, R.A., *Hyphal structures in Hydnus II. - Kon. Ned. Akad. v. Wetensch. C* 66: 426-457. 1963.
- MACHOL, R.E. & R. SINGER, *Bayesian analysis of generic relations in Agaricales. - Nova Hedwigia* 21: 753-787. 1971 (publ. 1972).
- MAIRE, R., *De l'utilisation des données cytologiques dans la taxonomie des Basidiomycètes. - Bull. Soc. Bot. Fr.* 1901.
- MAIRE, R., *Recherches cytologiques et taxonomiques sur les Basidiomycètes. - Bull. Soc. Myc. Fr. sep.* issue 18: 1-212, pl. 1-8. 1902.
- MAIRE, R., *Les bases de la classification dans le genre Russula. - Bull. Soc. Myc. Fr.* 26: 1-77. 1910.
- MAIRE, R., *Notes critiques sur quelques champignons. - Bull. Soc. Mycol. Fr.* 27: 403-458. 1911.
- MAIRE, R., *La flore mycologique des forêts de Cèdres de l'Atlas. - Bull. Soc. Myc. Fr.* 30: 199-229. 1914.
- MAIRE, R., *Champignons inédits de l'Afrique du Nord. - Bull. Soc. Myc. Fr.* 44: 37-56. 1928.
- MAIRE, R., *Études mycologiques. - I. Ann. Mycol.* 11: 331-338. 1913; II. *Bull. Soc. Myc. Fr.* 40: 293-316. 1924; III. *ibid.* 42: 40-42. 1926; IV. *ibid.* 46: 215-244. 1930.
- MAIRE, R., *Fungi Catalaunici. - Treb. Junta Mus. Ciènc. Nat. Barcelona* 3(2): 1-120, pl. 1. 1933.
- MAIRE, R., *Fungi Catalaunici, series altera. - Publ. Inst. Bot. Barcelona* 3(4): 1-128. 1937.
- MAIRE, R. & R. KÜHNER, *Deux agarics ochrosporés peu connus. - Bull. Soc. Myc. Fr.* 51: 192-203. 1935.
- MALENÇON, G., *Observations sur les ornements des spores chez les champignons. - Arch. Bot.* 3: 121-129, pl. 3. 1930.
- MALENÇON, G., *La série des Asteroporées. - Trav. Crypt. déd. à L. Mangin*, pp. 337-396, pl. 29. 1931.
- MALENÇON, G., *Considerations sur les spores des Russules et Lactaires. - Bull. Soc. Myc. Fr.* 47: 72-86. 1931.
- MALENÇON, G., *Dodgea occidentalis Malençon nouveau genre et nouvelle espèce de Rhizopogoneae. - Bull. Soc. Myc. Fr.* 54: 193-203. 1938.
- MALENÇON, G., *Le développement du Torrendia pulchella Bres. .... - Rev. Mycol.* 20: 81-130. 1955.
- MALENÇON, G., *Remarques sur les spores de quelques Rhodocybe. - Bull. Soc. Nat. d'Oyonnax* 12-13: 1-10. 1959.
- MALENÇON, G. & R. BERTAULT, *Flore des Champignons supérieurs du Maroc I-II.* Rabat 1970-1975.
- MALKOVSKY, K.M., *Über die europäischen Arten der Gattung Panus. - Ann. Mycol.* 30: 10-80. 1932.
- MALLOCH, D.W., K.A. PIROZYNKI & P.H. RAVEN, *Ecological and evolutionary significance of mycorrhizal symbiosis in vascular plants (a review). - Acad. Sci. USA* 77: 2113-2118. 1980.
- MANIOTIS, J., *The coprinoid state of Rhacophyllus lilacinus. - Am. J. Bot.* 51: 485-494. 1964.
- MARTIN, G.W., *On Lentoidum squamulosum. - Proc. Iowa Acad. Sc.* 63: 280-286. 1956.
- MATSUTAKE RESEARCH ASSOCIATION. *Matsutake - Kyoto.* pp. 1-223, 1964.
- MAUBLANC, A. & G. MALENÇON, *Recherches sur le Battarraea Guicciardiana Ces. - Bull. Soc. Myc. Fr.* 46: 43-72. 1930.
- MAUBLANC, A. & E. RANGEL, *Le Stilbum flavidum Cooke, forme avortée de l'Omphalia flava n. sp. - Bull. Soc. Mycol. Fr.* 30: 41-47. 1914.
- McDOUGALL, W.B., *The development of Stropharia empimyces. - Bot. Gaz.* 67: 258-263. 1919.
- MC LAUGHLIN, D.J., *Environmental control of fruitbody development in Boletus rubinellus in axenic culture. - Mycologia* 62: 307-331. 1970.
- McNABB, R.F.R., *The Strobilomycetaceae of New Zealand. - N.Z. Journ. Bot.* 5: 532-547. 1967.

- McNABB, R.F.R., *The Boletaceae of New Zealand*. - N.Z. Journ. Bot. 6: 137-167. 1968.  
 McNABB, R.F.R., *The Paxillaceae of New Zealand*. - N.Z. Journ. Bot. 7: 349-362. 1969.  
 MELZER, V., *Contribution à l'étude microscopique des Russules*. - Bull. Soc. Myc. Fr. 50: 218-225. 1934.  
 MELZER & J. ZVÁRA, *České Holubinky*. - Arch. Prirodo v. vyzkum Čech. 17: 1-126. 1927.  
 MÉTROD, G., *Quatre petits Pleurotes blancs*. - Rev. Myc. 3: 78-84. 1938.  
 MÉTROD, G., *Descriptions d'espèces du genre Clitocybe*. - Bull. Soc. Mycol. Fr. 55: 99-113. 1939.  
 MÉTROD, G., *Quelques espèces du genre Tricholoma*. - Rev. Mycol. 4: 101-118. 1939.  
 MÉTROD, G., *Sur le genre Melanoleuca*. - Rev. Mycol. 7: 89-96. 1942.  
 MÉTROD, G., *Les Tricholomes*. - Rev. Mycol. 7: Suppl. 1-50. 1942.  
 MÉTROD, G., *Les Clitocybes*. - Rev. Mycol. 14: Suppl. S4-S37. 1949.  
 MICKA, K., *Nové chemické reagencie v mikologii*. - Česk. Mikol. 8: 165-167. 1954.  
 MICKA, K. & J. KLÁN, *Chemical spot tests of macromycetes with benzidine*. - Česká Mykologie 34: 74-81. 1980.  
 MILLER, O.K., *Monograph of Chroogomphus*. - Mycologia 56: 526-549. 1964.  
 MILLER, O.K., *A revision of the genus Xeromphalina*. - Mycologia 60: 156-188. 1968.  
 MILLER, O.K., *A new species of Pleurotus ...* - Mycologia 61: 887-893. 1969.  
 MILLER, O.K., *The genus Panellus in North America*. - Mich. Bot. 9: 17-30. 1970.  
 MILLER, O.K., *The relationship of cultural characters to the taxonomy of the agarics* in PETERSEN (1971b), pp. 197-215.  
 MÖLLER, F.H., *Danish Psalliota species*. - Friesia 4: 1-60; 135-220. 1950-2.  
 MÖLLER, F.H., *The genus Leucopaxillus in Denmark*. - Bot. Tidsskr. 51: 233-241. 1954.  
 MÖLLER, F.H., *Fungi of the Faroes* 1-2, pp. 1-295. and 1-286. Einar Munksgaard, Copenhagen 1945-58.  
 MOORE, D., M.M.Y. ELHITI & R.D. BUTLER, *Morphogenesis of the carpophore of Coprinus cinereus*. - New Phytol. 83: 695-722. 1979.  
 MOREAU, F., *Étude histologique de la bulbilose des lames chez un Agaric*. - Bull. Soc. Myc. Fr. 29: 341-344. 1913.  
 MOSER, M., *Die Gattung Rozites*. - Schweiz. Zeitschr. Pilzk. 31: 164-172. 1953.  
 MOSER, M., *Blätter- und Bauchpilze in GAMS*, H., *Kleine Kryptogamenflora von Mitteleuropa II/b 2*, pp. 1-282. Gustav Fischer, Jena 1953. - 3. Auflage, pp. i-xii, 1-443. Gustav Fischer, Stuttgart 1967. 4. Auflage, pp. i-xiii, 1-532, 1978. - 5. Auflage pp. i-xiii, 1-533, 1983.  
 MOSER, M., *Studien zur Gattung Oudemansiella Spieg.*, Schleim- und Sammetrüblinge. - Zeitschr. f. Pilzk. 19: 4-11, 1955.  
 MOSER, M., *Die Gattung Phlegmacium (Schleimköpfe)* in *Die Pilze Mitteleuropas* 4: 1-440. Julius Klinkhardt, Bad Heilbrunn 1960 (publ. 1961).  
 MOSER, M., *Zur Variabilität von Leucopaxillus mirabilis (Bres.) Mos.* - Schweiz. Zeitschr. Pilzk. 41: 181. 1963.  
 MOSER, M., *Das System der Agaricales im Lichte neuerer Forschung*. - Ber. Deutsche Bot. Ges. 77: Sondernummer (101-109). 1964.  
 MOSER, M., *Corticarius Fr.*, Untergattung *Leprocyebe* subgen. nov., die Rauhköpfe. Vorstudien zu einer Monographie. - Zeitschr. Pilzk. 36: 37-57. 1970.  
 MOSER, M., *Moderne Aspekte der Mykologie*. - Zeitschr. f. Pilzk. 39: 39-44. 1973.

- MOSER, M. & E. HORAK, *Cortinarius und nahe verwandte Gattungen in Südamerika*. - Nov. Hedw., Beih. 52: 1-628, 131 plts. 1975.
- MOSS, E.H., *Developmental studies in the genus Collybia*. - Trans. R. Can. Inst. 14 prt. 2: 321-332. 1923.
- MUELLER, G.M. & W.J. SUNDBERG, *A floristic study of Laccaria (Agaricales) in Southern Illinois*. - Nov. Hedw. 34: 577-597. 1981.
- MURRILL, W.A., *North American flora* 9: 1-542. 1907-16; 10(1-5): 1-348. 1914-32 (some genera by Kauffman, Overholts, Pennington, Burlingham).
- NEUHOFF, W., *Das System der Blätterpilze*. - Zeitschr. f. Pilzk. 21: 10. 1952.
- NEUHOFF, W., *Die Milchlinge in Die Pilze Mitteleuropas* 2b: 1-248. Julius Klinkhardt, Bad Heilbrunn 1956.
- NOBLES, M., *Cultural characters as a guide to the taxonomy and phylogeny of the Polyporaceae*. - Canad. Journ. Bot. 36: 883-926. 1958.
- NOBLES, M., *Cultural characters as a guide to the taxonomy of the Polyporaceae* in R.H. PETERSEN (1971b), pp. 169-196.
- NOORDELOOS, M.E., *Introduction to the taxonomy of the genus Entoloma sensu lato (Agaricales)*. - Persoonia 11: 121-151. 1981.
- NUSS, I., *Untersuchungen zur systematischen Stellung der Gattung Polyporus*. - Hoppea 39: 127-198. 1980.
- OBERWINKLER, F., *Die Gattungen der Basidiolichenen*. - Ber. Deutsch. Bot. Ges. N. F. 4: 139-169. 1970.
- OLA'H, G.M., *Le genre Panaeolus*. - Rev. Mycol. Mém. hors série 10: i-vii, 1-222, 1969.
- ORTON, P.D., *New Check List of British Agarics and Boleti*, part 3, Notes ... - Trans. Brit. Mycol. Soc. 43: 159-439. 1960.
- ORTON, P.D., *Notes on British Agarics. III. - Notes Roy. Bot. Gard. Edinburgh* 29: 75-127. 1969.
- ORTON, P.D. & R. WATLING, *A reconsideration of the classification of the Hygrophoraceae*. - Notes Roy. Bot. Gard. Edinburgh 29: 129-138. 1969.
- OVEREEM, C. VAN & J. WEESE, *Icones fungorum Malayensium*. Heft I-XV. Wien 1923-6.
- OVERHOLTS, L.O., see also under Murrill.
- OVERHOLTS, L.O., *A monograph of the genus Pholiota in the United States*. - Ann. Missouri Bot. Gard. 14: 87-210. 1927.
- PANTIDOU, M.E., *Cultural studies of Boletaceae. Gyrodon meruloides and four species of Boletinus*. - Can. J. Bot. 39: 1149-1162. 1961.
- PANTIDOU, M.E., *Cultural studies of Boletaceae: Carpophores of Xerocomus badius and Xerocomus illudens in culture*. - Can. J. Bot. 42: 1147-1149. 1964.
- PANTIDOU, M.E. & J.W. GROVES, *Cultural studies of Boletaceae. Some species of Suillus and Fusco-boletinus*. - Can. J. Bot. 44: 1371-1392. 1966.
- PASTAC, I.A., *Les matières colorantes des champignons*. - Rev. Myc. Mém. hors-série no. 2, pp. I-III, 1-88, 1942.
- PATOUILARD, N., *Sur quelques modes nouveaux ... de reproduction secondaire ...* Rev. Myc. 3: 30. 1881.
- PATOUILARD, N., *Quelques observations sur l'hyménium des Basidiomycètes*. - Rev. Myc. 5: 1. 1883.
- PATOUILARD, N., *Quelques points de la classification des Agaricinées*. - Journ. Bot. 2: 12-16. 1888.
- PATOUILARD, N., *Tabulae analyticae fungorum*. 1-9: no. 1-700, Paris 1883-9.

- PATOUILlard, N., *Sur la place du genre Favolus*. - *Bull. Soc. Myc. Fr.* 6: xix. 1890.
- PATOUILlard, N., *Le genre Phlebophora Lév.* - *Bull. Soc. Myc. Fr.* 10: 75-81. 1894.
- PATOUILlard, N., *Variations du sclérite de Lentinus Woermannii Cohn & Schroet.* - *Bull. Soc. Myc. Fr.* 11: 247. 1895.
- PATOUILlard, N., *Le genre Skepperia Berk.* - *Bull. Soc. Fr.* 11: 13. 1895.
- PATOUILlard, N., *Champignons de la Guadeloupe*. - *Bull. Soc. Mycol. Fr.* 15: 191-209. 1899.
- PATOUILlard, N., *Essai taxonomique sur les familles et les genres des Hyménomycètes*, pp. 1-184. Lons-le-Saunier 1900.
- PATOUILlard, N., *Champignons Algéro-Tunisiens nouveaux et peu connus*. - *Bull. Soc. Mycol. Fr.* 17: 182-188. 1901.
- PATOUILlard, N., *Polypores à cystides étoilés*. - *Bull. Soc. Mycol. Fr.* 30: 36-40. 1914.
- PEGLER, D.N., *Studies on African Agaricales*. - *Kew Bull.* 23: 219-249. 1969.
- PEGLER, D.N., *Revision of the genus Lepiota from Ceylon*. - *Kew Bull.* 27: 155-202. 1972.
- PEGLER, D.N. & R.W. RAYNER, *A contribution to the agaric flora of Kenya*. - *Kew Bull.* 23: 347-412. 1969.
- PEGLER, D.N., *The polypores*. 2nd ed. *Bull. Brit. Myc. Soc. Suppl.* 7pp 1-43. 1973.
- PEGLER, D.N., *A preliminary agaric flora of East Africa*. - *Kew Bull. add. ser.* 6: 1-615. 1977.
- PEGLER, D.N., *Agaric flora of the Lesser Antilles*. - *Kew Bull., add. ser.* 9: 1-668, 27 plts. 1983.
- PEGLER, D.N., *The genus Lentinus*. - *Kew Bull. add. ser.* 10: 1-281. 1983.
- PEGLER, D.N. & R.W. RAYNER, *A contribution to the agaric flora of Kenya*. - *Kew Bull.* 23: 347-412. 1969.
- PEGLER, D.N., B.M. SPOONER & R.I. LEWIS SMITH, *Higher fungi of Antarctica*. - *Kew Bull.* 35: 499-562. 1980.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore Morphology in the Agaricales*. - *Beih. Nova Hedwigia* 35. 1971.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Inocybe*. - *Kew Bull.* 26: 499-537. 1972.
- PEGLER, D.N. & T.W.K. YOUNG, *Reassessment of the Bondarzewiaceae (Aphyllophorales)*. - *Trans. Brit. Myc. Soc.* 58: 49-58. 1972.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Crepidotus*. - *Kew Bull.* 27: 311-323. 1972.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Galerina and Kuehneromyces*. - *Kew Bull.* 27: 483-500. 1972.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Leucopaxilleae*. - *Kew Bull.* 28: 365-379. 1973.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Clitopilus, Rhodocybe, and Rhodotus*. - *Kew Bull.* 30: 19-32. 1975.
- PEGLER, D.N. & T.W.K. YOUNG, *Basidiospore form in the British species of Naucoria, Simocybe, and Phaeogalera*. - *Kew Bull.* 30: 225-240. 1975.
- PEGLER, D.N. & T.W.K. YOUNG, *Entolomataceae Kotl. & Pouz. in World Pollen and Spore Flora 7* (S. Nilsson, ed.): 1-24. 1978.
- PEGLER, D.N. & T.W.K. YOUNG, *Spore form and phylogeny of Entolomataceae*. - *Sydowia Beih.* 8: 290-303. 1979.

PEGLER, D.N. & T.W.K. YOUNG, *The gasteroid Russulales*. - *Trans. Brit. Myc. Soc.* 72: 353-388. 1979.

PENNINGTON, (see Murrill).

PERREAU, J., *Recherches sur les ornements sporales et la sporogenese chez quelques espèces des genres Boletellus et Strobilomyces (Basidiomycetes)*. - *Ann. Soc. Nat. Bot.* 12 ser.: 393-489. 1961.

PERREAU, J., *Complément à l'étude des ornements sporales dans le genre Boletellus*. - *Ann. Sci. Nat. (Bot.)* XII 5: 753-766. 1964.

PERREAU, J. *Recherches sur la differenciation et la structure de la paroi sporale chez les Homobasidio-mycètes a spores ornées*. - *Ann. Sci. Nat. Biol.* 12e ser. vol. 8: 639-746. 1967.

PERREAU, J., *Variations sur un thème ornemental: Le réseau des basidiospores*. - *Travaux dédiés à R. Kühner. Bull. Soc. Linn. Lyon*, no. spécial pp 63-84. 1974.

PERREAU, J. & R. HEIM, *L'ornementation des basidiospores au microscope electronique à balayage*. *Rev. Mycol.* 33: 329-340.

PERREAU-BERNARD, J. & L.M. MELENDEZ-HOWELL, *Observations sur la structure tegumentaire sporale de quelques basidiomycètes chromospores*. - *C.R. Acad. Sc. Paris* 262: 454-457. 1966.

PETERSEN, R.H., *The genera Gomphus and Gloeocantharellus in North America*. 112 pp., 4 pls. Lehre 1971 (a).

PETERSEN, R.H., *Interfamiliar relationships in the clavarioid and cnatharelloid fungi in: The Evolution of the Higher Basidiomycetes*. Knoxville 1971 (b).

PETRI, L., *Lo sviluppo del corpo fruttifero del Hydnangium carneum Wallr.* - *Rendiconti Cong. Bot. di Palermo* 1902. 148-151. 1902.

PILÁT, A., *Skepperia carpatica sp. n. nouvelle espèce intéressante du genre Skepperia Berk. dans les Carpathes Centrales*. - *Bull. Soc. Mycol. Fr.* 43: 49-58. 1927.

PILÁT, A., in KAVINA, K. & A. PILÁT, *Atlas des champignons de l'Europe: Pleurotus*. Praha 1935.

PILÁT, A., *Über eine neue interessante Art aus der Gattung Crepidotus*. - *Hedwigia* 49: 137-147. 1929.

PILÁT, A., *Revision der tropischen Lentinus-Arten aus dem Herbar des Botanischen Museums in Berlin-Dahlem*. - *Ann. Mycol.* 34: 108-140. 1936.

PILÁT, A., in KAVINÁ, K. & A. PILÁT, *Atlas des champignons de l'Europe 5: Monographie des espèces européennes du genre Lentinus*. pp. 1-46. 1946; 6: *Monographie des espèces européennes du genre Crepidotus* Fr.. pp. 1-83. 1948.

PILÁT, A., *Revision of the types of the extraeuropean species of the genus Crepidotus*. - *Trans. Brit. Mycol. Soc.* 33: 215-249. 1950.

PILÁT, A., *The Bohemian species of the genus Agaricus*. - *Act. Mus. Nat. 7B*: 1-142. 1951.

PILÁT, A. & A. DERMEK, *Hribováte huby*. Bratislava, 1974.

PILÁT, A. & M. SVRČEK, *O meším oušku sivém - Leptotus glaucus - ve smyslu Batschově - Friesově a Quéletově i pozdějších autorů*. - *Česká Mikologie* 7: 8-12. 1953.

PIROZYNISKI, K.A., *Pacific Mycogeography: An appraisal*. - *Austral. J. Bot.*, Suppl. ser. 10: 137-159. 1983.

POELT, J., *Eine Basidiolichene in den Hochalpen*. - *Planta* 52: 600-605. 1959.

POELT, J. & W. JÜLICH, *Omphalina grisella, ein weiterer lichenisierter Blätterpilz in den Alpen*. - *Herzogia* 1: 331-336. 1969.

POELT, J. & F. OBERWINKLER, *Zur Kenntnis der flechtenbildenden Blätterpilze der Gattung Omphalina*. - *Österreich. Bot. Zeitschr.* 111: 393-401. 1964.

POUCHET, A., *Considérations sur Rhodotus patmatus*. - *Bull. Soc. Myc. Fr.* 48: 76-83, pl. 11. 1932.

- POUZAR, Z., *Amyloidity in polypores I. The genus Polyporus* Mich. ex Fr. - Česk. Myk. 26: 82-90. 1972.
- QUÉLET, L., *Enchiridion fungorum in Europa et praesertim in Gallia vigentium*, p. I-IV, 1-352. 1886.
- QUINTANILHA, A., *Le problème de la sexualité chez les champignons*. Coimbra 1933. (Reprint Lehre 1968).
- QUINTANILHA, L. & A. VASERMANIS, *La conduite sexuelle et la systématique des Hyménomycètes*. - Rev. de Mycol. 6: 3-48. 1941.
- RAPER, J.R., *Genetics of Sexuality in Higher fungi*. The Ronald Press Co., New York i-viii, 1-283. 1966.
- RAWALD, W., *Das Artproblem bei höheren Pilzen in physiologischer Sicht*. - Zeitschr. f. Pilzk. 27: 69-78. 1961.
- REDHEAD, S.A., *Physalacria subpeltata sp. nov. from Hawaii*. - Mycotaxon 10: 46-48. 1979.
- REDHEAD, S.A., *The genus Strobilurus (Agaricales) in Canada*... - Can. J. Bot. 58: 68-83. 1980.
- REDHEAD, S.A., *Parasitism of bryophytes by agarics*. - Can. J. Bot. 59: 63-67. 1981.
- REDHEAD, S.A., *The application of Helotium to agarics*. - Can. J. Bot. 60: 1998-2018. 1982.
- REDHEAD, S.A., *Additional Agaricales on wetland Monocotyledones in Canada*. - Can. J. Bot. 62: 1844-1851. 1984.
- REDHEAD, S.A., *Mycological observations 13-14 on Hypsizygus and Tricholoma*. - Trans. Myc. Soc. Japan 25: 1-9. 1984.
- REDHEAD, S.A., *Arrhenia and Rimbachia, expanded generic concepts and a re-evaluation of Leptoglossum*. - Can. J. Bot. 62: 865-892. 1984.
- REDHEAD, S.A. & J.H. GINNS, *A reappraisal of agaric genera associated with brown rots of wood*. - Trans. Myc. Soc. Japan 26: 349-381. 1985.
- REDHEAD, S.A. & R. SINGER, *Resinomycena gen. nov.* ... - Mycotaxon 13: 150-170. 1981.
- REDHEAD, S.A. & L.K. WERESUB, *On Omphalia and Omphalina*. - Mycologia 70: 556-568. 1978.
- REID, D.A., *Fungi Venezuelan I. The Cyphellaceae of Venezuela*. - Kew Bull 15: 261-275. 1961.
- REID, D.A., *Notes on some fungi of Michigan. I. Cyphellaceae*. - Persoonia 3: 97-154. 1963.
- REID, D.A., *A monograph of the stipitate stereoid fungi*. - N. Hedw. Beih. 18: 1-376. 1965.
- REID, D.A., *Intermediate generic complexes between the Thelephoraceae and other families* in PETERSEN (1971b).
- REID, D.A., *Type studies of the larger Basidiomycetes described from South Africa*. - Contr. Bolus Herb. 7: i-iv, 1-255. 1975.
- REININGER, W., W. STEGLICH & M. MOSER, *Velumpigmente einiger Cortinarien der Unter-gattung Telamonia*. - Zeitschr. Naturf. 27b: 1099. 1972.
- REIJNDERS, A.F.M., *Studies van de Ontwikkeling van de Basidiocarpen der Agaricales*. - Medd. Ned. Myc. Ver., 1933.
- REIJNDERS, A.F.M., *Études sur le développement et l'organisation histologique des carpophores dans les Agaricales*. - Rev. trav. bot. Néerl. 41: 213-396. 1948.
- REIJNDERS, A.F.M., *Recherches sur le développement des carpophores dans les Agaricales*. - Verh. Kon. Nederl. Akad. Wet. Afd. Naturrk. II. 48: 1-116. 1952.
- REIJNDERS, A.F.M., *Les problèmes du développement des carpophores des Agaricales et de quelques groupes voisins*. Den Haag, pp. 1-412. 1963.
- REIJNDERS, A.F.M., *Le développement de deux espèces de Cortinariaceae*... - Bull. Soc. Linn. Lyon 43: 355-464. 1979.
- REIJNDERS, A.F.M., *The development of three species of the Agaricaceae*... - Persoonia 8: 307-319. 1975.

- REIJNDERS, A.F.M., *Recherches sur le développement et l'histogenèse dans les Astérosporales*. - *Persoonia* 9: 65-83. 1976.
- REIJNDERS, A.F.M., *The histogenesis of bulb and trama tissue of the Higher Basidiomycetes*. *Persoonia* 9: 329-362. 1977.
- REIJNDERS, A.F.M., *On carpophore development in the genera Cortinarius, Dermocybe and Leucocortinarius*. - *Sydotia Beih.* 8: 335-348. 1979 (a).
- REIJNDERS, A.F.M., *Developmental anatomy of Coprinus*. - *Persoonia* 10: 383-424. 1979(b).
- REIJNDERS, A.F.M., *Le développement de Limacella glioderma (Fr.) R. Maire*. - *Persoonia* 10: 301-308. 1979(c).
- REIJNDERS, A.F.M., *Le développement de Tectella patellaris (Fr.) Murr.* - *Bull. Soc. Myc. Fr.* 99: 109-126. 1983.
- REIJNDERS, A.F.M., *Supplementary notes on basidiocarp ontology in agarics*. - *Persoonia* 12: 1-20. 1983.
- REIJNDERS, A.F.M., *Le développement d'Hygrotrama atropuncta (Pers.: Fr.) Sing.* - *Cryptogamie-Mycologie* 4: 71-78. 1983.
- REIJNDERS, A.F.M. & G. MALENÇON, *Recherches sur le développement d'une espèce appartenant au genre Rhacophyllus Berk. et Br.* - *Bull. Soc. Myc. Fr.* 85: 295-304. 1969.
- RIOUSSET, L., M. JOSSEYRAN & A. CAPELLANO, *Position systématique et description de Rhodocybe stangliana (= Squamanita stangliana)* ... *Bull. Soc. Linn. Lyon* 46: 119-130. 1977.
- ROGERS, D.P., *Relative dates of S.F. Gray's Natural Arrangement and Fries' Systema*. - *Mycologia* 33: 568-570. 1941.
- ROLLAND, L., *De la coloration en bleu développée par l'iode sur divers champignons et notamment sur un agaric*. - *Bull. Soc. Myc. Fr.* 3: 134. 1887.
- ROMAGNESI, H., *Sur le Rhodophyllus*. - *Bull. Soc. Myc. Fr.* 49: 422-438. 1933.
- ROMAGNESI, H., *Essai d'une classification générique des agarics Ianthinosporés et Melanosporés*. - *Rev. Myc.* 1: 27-36. 1936.
- ROMAGNESI, H., *Sur l'expression mathématique de l'écartement des lamelles chez les Agarics*. - *Bull. Soc. Myc. Fr.* 52: 261-270. 1936.
- ROMAGNESI, H., *Florule mycologique des Bois de la Grange et de l'Etoile*. - *Rev. Mycol.* 2-4, 1937-9, especially 2: 20-38. 1937.
- ROMAGNESI, H., *Essai d'un sectionnement du genre Rhodophyllus*. - *Bull. Soc. Myc. Fr.* 53: 319-338. 1937.
- ROMAGNESI, H., *A la recherche de Lactarius subdulcis*. - *Bull. Soc. Myc. Fr.* 54: 204-225. 1938.
- ROMAGNESI, H., *Sur le genre Drosophila Quél.* - *Rev. Mycol.* 4: 119-130. 1939.
- ROMAGNESI, H., *Mycenella et Xerula*. - *Bull. Soc. Myc. Fr.* 56: 59-65. 1940.
- ROMAGNESI, H., *Une nouvelle Russule du groupe «Integra»*. - *Bull. Soc. Myc. Fr.* 56: 65-70. 1940.
- ROMAGNESI, H., *Essai sur le genre Tubaria W. Sm.* - *Rev. Mycol.* 5: 28-43. 1940.
- ROMAGNESI, H., *Essai sur le genre Tubaria W. Sm.* - *Rev. Mycol.* 5: 28-43. 1940.
- ROMAGNESI, H., *Les Rhodophylles de Madagascar*, pp. 9-164. Paris 1941.
- ROMAGNESI, H., *Descriptions de quelques espèces d'Agarics ochrosporés*. - *Bull. Soc. Myc. Fr.* 58: 112-149. 1942.
- ROMAGNESI, H., *Quelques points de taxonomie*. - *Bull. Soc. Myc. Fr.* 55: 81-89. 1942.
- ROMAGNESI, H., *Études complémentaires sur le genre Tubaria*. - *Rev. Mycol.* 8: 27-35. 1943.
- ROMAGNESI, H., *La cystide chez les Agaricacées*. - *Rev. Mycol.*, Suppl., pp. 4-21. 1944.

- ROMAGNESI, H., *Classification du genre Drosophila Quél.* - Bull. Soc. Linn. Lyon 13: 51-54. 1944.
- ROMAGNESI, H., *Contribution à l'étude des Russules de la flore française*. - I. Bull. Soc. Myc. Fr. 48: 150-169. 1942; II. ibid. 49: 61-71. 1943; III. ibid. 61: 22-37. 1945.
- ROMAGNESI, H., *Étude de la structure de la trame chez quelques Pleurotacés*. - Bull. Soc. Myc. Fr. 61: 38-46. 1945.
- ROMAGNESI, H., *Les problèmes et les méthodes de la systématique ...* Bull. Soc. Myc. Fr. 64: 1-47. 1948.
- ROMAGNESI, H., *Sur les rapports des Cyphellinées avec certains groupes d'Agaricales*. - Proc. VII. Intern. Bot. Congress Stockholm, pp. 407-410. 1951.
- ROMAGNESI, H., *Quelques Omphalia des sables maritimes fixés*. - Rev. d. Mycol. 17: 39-45. 1952.
- ROMAGNESI, H., *A propos de la monographie des Lactaires de W. Neuhoff*. - Bull. Soc. Myc. Fr. 72: 324-340. 1956.
- ROMAGNESI, H., *Les Russules d'Europe et de l'Afrique du Nord* Bordas. 998 pp., 1967.
- ROMAGNESI, H., *Essai d'une classification des Rhodophylles*. - Bull. Soc. Linn. Lyon 43: 325-332. 1974.
- ROMAGNESI, H., *Observations sur la structure et le développement des voiles chez les Psalliotes à l'état postprimordial et adulte*. - Bull. Soc. Myc. Fr. 93: 5-19. 1977.
- ROMAGNESI, H., *Les fondements de la taxonomie des Rhodophylles et leur classification*. Cramer, Vaduz, 1978.
- ROMAGNESI, H., *Etudes complémentaires de quelques espèces de Psathyrella ss. lato (Drosophila Quél.)* - Bull. Soc. Myc. Fr. 98: 5-68. 1982.
- ROMAGNESI, H. & H. MARXMÜLLER, *Étude complémentaire sur les Armillaires annelées*. - Bull. Soc. Myc. Fr. 99: 301-324. 1983.
- ROSINSKY, M.A. & A.D. ROBINSON, *Hybridization of Panus tigrinus and Lentodium squamulosum*. - Amer. J. Bot. 55: 242-246. 1968.
- SASS, J.E., *The cytological study of a bispored form of Psalliota campestris*. - Pap. Mich. Acad. Sci. 9: 287-298. 1928.
- SASS, J.E., *The cytological basis of homothallism and heterothallism in the Agaricaceae*. - Amer. Journ. Bot. 16: 663-701. 1929.
- SATHE, A.V. et al., *Agaricales (mushrooms) of South West India*, ser. 1. - Macs Monogr. 1: i-vii, 1-114. 1980.
- SAUTTER, C., *Vergleichende morphologische und anatomische Untersuchungen an Polyporaceen*. Dissertation, Tübingen 1978.
- SAVILE, D.B.O., *A phylogeny of the Basidiomycetes*. - Can. Journ. Bot. 33: 60-104. 1955.
- SAWYER, W.H., *The development of Cortinarius pholidaeus*. - Amer. Journ. Bot. 4: 520-532. 1917.
- SAWYER, W.H., *The development of some species of Pholiota*. - Bot. Gaz. 64: 206-229. 1917.
- SCHÄFFER, J. & F. MÖLLER [F.H. MÖLLER], *Beitrag zur Psalliota-Forsch.* - Ann. Mycol. 36: 64-82. 1938.
- SCHWANTES, H.O. & E. GEßNER, *Untersuchungen zur Fruchtkörperbildung von Lentinus tigrinus (Bull. ex Fr.) Fr. und Polyporus melanopus (Swartz ex Fr.) Fr. .... Biol. Zentralbl.* 93: 561-570. 1974.
- SINGER, R., *Beitrag zur systematischen Stellung des Crepidotus nidulans*. - Arch. Prot.-Kunde 65: 314-320. 1929.
- SINGER, R., *Monographie der Gattung Russula*. - Beih. Bot. Centralbl. 49(II): 205-380. 1932.
- SINGER, R., *Étude systématique sur les Melanoleuca d'Europe et clé des espèces observées en Catalogne*. - Cavanillesia 7: 123-132. 1935.

- SINGER, R., *Studien zur Systematik der Basidiomyceten*. - *Beih. Bot. Centralbl.* 56(B): 137-174. 1936.
- SINGER, R., *Contribution à l'étude des Russules III*. - *Bull. Soc. Myc. Fr.* 54: 132-177. 1938.
- SINGER, R., *Sur les genres Ixocomus, Boletinus, Phylloporus, Gyrodon et Gomphidius*. - *Rev. Mycol.* 3: 35-53, 157-177, pl. 4. 1938.
- SINGER, R., *De nonnullis Basidiomycetibus. Notulae Systematicae e Sect. Cryptog. Inst. e Bot. Acad. Sc. U.S.S.R.* 10-12. 1938.
- SINGER, R., *O novykh danniyh dlja sistematiki i filogenii Agaricales kak potomkov Gastromycetes*. - *Sov. Bot.* 1939(1): 95-98. 1939.
- SINGER, R., *Notes sur quelques Basidiomycètes*. - *Rev. Mycol.* 1: 75-84. 1936; 1: 279-293. 1936; 2: 226-242; 3: 31. 1938; 3: 187-199. 1938; 4: 65-72. 1939; 5: 3-13. 1940.
- SINGER, R., *A monographic study of the genera "Crinipellis" and "Chaetocalathus"*. - *Lilloa* 8: 441-534. 1942.
- SINGER, R., *Das System der Agaricales*. - I. *Ann. Myc.* 34: 286-378. 1936; II. *Ann. Myc.* 40: 1-132. 1942; III. *Ann. Myc.* 41: 189. 1943.
- SINGER, R., *Notes on taxonomy and nomenclature of the Polypores*. - *Mycologia* 36: 65-69. 1944.
- SINGER, R., *The Laschia-complex*. - *Lloydia* 8: 170-230. 1945.
- SINGER, R., *New and interesting species of Basidiomycetes*. - I. *Mycologia* 37: 425-439. 1945; II. *Mich. Acad. Sc. Arts Lett.* 32: 103-150. 1948; III. *Sydowia* 4: 130-157. 1950; IV. *Mycologia* 47: 763-777. 1955; V. *Sydowia* 11: 141-272. 1957; VI. *Mycologia* 51: 375-400. 1959 (publ. 1960); VII. *Mycologia* 51: 578-594. 1959 (publ. 1960).
- SINGER, R., *Notes on Farlow's Agaricales from Chocorua*. - *Farlowia* 2: 39-52. 1945.
- SINGER, R., *Type studies on Agarics*. - I. *Lloydia* 5: 97-135. 1942; II. *Lloydia* 9: 114-131. 1946; III. *Lilloa* 25: 463-514. 1952.
- SINGER, R., *The Boletineae of Florida with notes on extralimital species*. - I. *Farlowia* 2: 97-141. 1945; II. *Farlowia* 2: 223-303. 1945; III. *The Amer. Midl. Nat.* 37: 1-135. 1947; IV. *Farlowia* 2: 527-567. 1946.
- SINGER, R., *Two new species in the Agaricales*. - *Mycologia* 38: 687-690. 1946.
- SINGER, R., *Type studies on Basidiomycetes*. I. - *Mycologia* 34: 64-93. 1942; II. *Mycologia* 35: 142-163. 1943; III. *Mycologia* 39: 171-189. 1947; IV. *Lilloa* 23: 147-246. 1950 (publ. 1952); V. *Sydowia* 5: 445-475. 1951; VI. *Lilloa* 26: 57-159. 1953; VII. *Sydowia* 6: 344-351. 1952; VIII. *Sydowia* 9: 367-431. 1955; X. *Persoonia* 2: 1-62. 1961.
- SINGER, R., *Coscinoids and coscinocystidia in Linderomyces lateritius*. - *Farlowia* 3: 155-157. 1947.
- SINGER, R., *New genera of fungi*. - I. *Mycologia* 36: 358-368. 1944; II. *Lloydia* 8: 139-144. 1945; III. *Mycologia* 39: 77-89. 1947; IV. *Mycologia* 40: 262-264. 1948; V. *Mycologia* 43: 598-604. 1951; VI. *Lilloa* 32: 255-258. 1951; VII. *Mycologia* 48: 719-727. 1956; VIII. *Mycologia* 50: 103-110. 1958; IX. ("VIII") *Persoonia* 2: 407-415. 1962; X. *Sydowia* 11: 320-322. 1957; XI. *Lilloa* 30: 375-379. 1960.
- SINGER, R., *Contributions toward a monograph of the genus Crepidotus*. - *Lilloa* 13: 59-95. 1947.
- SINGER, R., *Diagnoses fungorum novorum Agaricalium*. - *Sydowia* 2: 26-42. 1948. - II. *ibid.* 15: 49-83. 1961.
- SINGER, R., *The genus Gomphidius Fries in North America*. - *Mycologia* 41: 462-489. 1949.
- SINGER, R., *Supplementary notes on Campanella and Favolaschra*. - *Lloydia* 13: 249-259. 1950.
- SINGER, R., *The Agaricales (Mushrooms) in modern taxonomy*. - *Lilloa* 22: 1-832. 1949 (publ. 1951). - 2nd. ed. Cramer 1962. - 3<sup>rd</sup> ed. Cramer, Vaduz 1975.
- SINGER, R., *The agarics of the Argentine sector of Tierra del Fuego...* - I. *Sydowia* 6: 165-226. 1952. - II. *Sydowia* 7: 206-265. 1953.

- SINGER, R., *Four years of mycological work in South America*. - *Mycologia* 45: 865-891. 1953.
- SINGER, R., *Le genre Gloiocephala* Massee. - *Rev. d. Mycol.* 17: 161-164. 1952.
- SINGER, R., *Fungi in N. POLUNIN, The Cryptogamic Flora of the Arctic VI*. - *Bot. Review* 20: 451-462. 1954.
- SINGER, R., *Agaricales von Nahuel Huapi*. - *Sydowia* 8: 100-157. 1954.
- SINGER, R., *Le genre Melanomphalia* Christiansen. - *Rev. d. Mycol.* 20: 12-17. 1955.
- SINGER, R., *Un Clitocybe cortiqué et un Clitocybe faux*. - *Bull. Soc. Mycol. Fr.* 71: 147-152. 1955.
- SINGER, R., *New species of Agaricales from Pernambuco*. - *An. Soc. Biol. Pern.* 13: 225-229. 1955.
- SINGER, R., *A fungus collected in the Antarctic*. - *Sydowia. Beih.* 1 (Festschr. f. Franz Petrak): 16-23. 1956.
- SINGER, R., *The Armillariella mellea group*. - *Lloydia* 19: 176-178. 1956.
- SINGER, R., *Versuch einer Zusammenstellung der Arten der Gattung Phaeomarasmius*. - *Schweiz. Zeitschr. f. Pilzk.* 34: 44-47, 53-65. 1956.
- SINGER, R., *Contributions towards a monograph of the genus Pluteus*. - *Trans. Brit. Mycol. Soc.* 39:145-232. 1956. - II. *Ibid.* 42: 223-226. 1959.
- SINGER, R., *Fungi Mexicanii, series prima, Agaricales*. - *Sydowia* 11: 354-374. 1957. - Series secunda, *Ibid.* 12: 221-243. 1958.
- SINGER, R., *Studies towards a monograph of the South American species of Marasmius*. - *Sydowia* 12: 54-148. 1958.
- SINGER, R., *The meaning of the affinity of the Secotiaceae with the Agaricales*. - *Sydowia* 12: 1-43. 1958.
- SINGER, R., *Mycological investigations on teonanácatl, the Mexican hallucinogenic mushroom I-II*. - *Mycological* 50: 239-303. 1958.
- SINGER, R., *Observations on agarics causing cerebral mycetisms*. - *Mycopathologia et Mycologia applicata* 9: 261-284. 1958.
- SINGER, R., *Dos géneros nuevos para Argentina*. - *Bol. Soc. Arg. Bot.* 8: 9-13. 1959.
- SINGER, R., *Basidiomycetes from Masatierra*. - *Ark. f. Bot.* II. 4(9): 371-400. 1959.
- SINGER, R., *Sobre algunas especies de hongos presumiblemente psicotropicos*. - *Lilloa* 30: 117-127. 1960.
- SINGER, R., *Monographs of South American Basidiomycetes I-X*. - *Lloydia* 21: 159-299. 1958; *Sydowia* 18: 106-358. 1965; 14: 258-290. 1960; 15: 112-132. 1961; *Bol. Soc. Arg. Bot.* 10: 57-67. 1962; *Darwiniana* 12: 598-611. 1963; *Nova Hedwigia* 7: 93-132. 1964; *Darwiniana* 13: 145-190. 1964; *Bol. Soc. Arg. Bot.* 10: 302-310. 1965.
- SINGER, R., *Three new species of secotiaceous fungi from Patagonia*. - *Persoonia* 1: 385-391. 1960.
- SINGER, R., *Fungi of Northern Brazil*. *Univ. Recife. Inst. Micol. publ.* 304: 3-26. 1961.
- SINGER, R., *Notes on secotiaceous fungi: Galeropsis and Brauniella*. - *Kon. Nederl. Akad. Wetensk. Proceed. C* 66: 106-117. 1963.
- SINGER, R., *Die Gattung Gerronema*. - *Nova Hedwigia* 7: 53-92. 1964.
- SINGER, R., *Skepperiella populi y la filogenia de las Cyphellaceae*. - *Bol. Soc. Arg. Bot.* 10: 209-214. 1965.
- SINGER, R., *Schlüssel zur Bestimmung der Familien und Gattungen der Basidiomyzetenordnung Agaricales*. Separatabdruck *Schweiz. Zeitschr. Pilzk.* 1-44. 1965-66.
- SINGER, R., *Notes on cyphellaceous fungi*. - *Darwiniana* 14: 9-18. 1966.

- SINGER, R., *Die Pilze Mitteleuropas. V. Die Röhrlinge*. Teil I, 1965. 1-129. Teil II. 1967, 1-151.
- SINGER, R., *Mycoflora Australis. - Beih. Nova Hedwigia* 29: 1-405. 1969.
- SINGER, R., *Monograph 3-4-5 in Flora Neotropica*, published for the OFN by Hafner, New York, 1970. - 17: *The New York Bot. Garden* 1976. - 32: *Ibid.* 1982.
- SINGER, R., *A revision of the genus Melanomphalia as a basis of the phylogeny of the Crepidotaceae*, in PETERSEN, R.H., *Evolution of the Higher Basidiomycetes*. Knoxville 1970.
- SINGER, R., *Forest mycology and forest communities in South America II*. in E. HACSKAYLO, *Mycorrhiza*. U.S. Government Printing Office, Washington 1971.
- SINGER, R., *Cyanophilous spore walls in the Agaricales and agaricoid Basidiomycetes*. - *Mycologia* 64: 822-829. 1972.
- SINGER, R., *Notes on Bolete taxonomy*. - *Persoonia* 7: 313-320. 1973; II: *Ibid.* 9: 421-438. 1978; III: *Ibid.* 11: 269-302. 1981.
- SINGER, R., *A monograph of Favolaschia*. - *Nov. Hedw. Beih.* 50: 1-108. 1974.
- SINGER, R., *The neotropical species of Campanella and Aphyllotus*. - *Nov. Hedw.* 26: 847-895. 1975.
- SINGER, R., *Interesting and new species of Basidiomycetes from Ecuador*. - Reprint of two parts, Cramer, Vaduz 1975.
- SINGER, R., *Tropical Russulaceae...* *Nov. Hedw.* 26: 897-901. 1975. - II: 40: 435-447. 1984.
- SINGER, R., *Amparoinaceae and Montagneaceae*. *Rev. Myc.* 40: 57-64. 1976.
- SINGER, R., *Die Gruppe der Laccaria laccata (Agaricales)*. - *Plant Syst. Evol.* 126: 347-370. 1977.
- SINGER, R., *An interpretation of Palaeosclerotium*. - *Mycologia* 69: 850-854. 1977.
- SINGER, R., *Amerikanische und Asiatische Agaricales, die in Europa und Nordafrika vorkommen*. - *Zeitschr. f. Pilzk.* 43: 119-130. 1977.
- SINGER, R., *New genera of Agaricales*. - *Mycologia* 73: 500-510. 1981.
- SINGER, R., *Acanthocytes in Amparoina and Mycena*, - *Cryptogamie, Mycologie* 4: 111-115. 1983.
- SINGER, R., *The role of fungi in Amazonian forests and in reforestation*. In: H. Sioli (ed.). *The Amazon*. Junk, Dordrecht/Boston/Lancaster. 1984.
- SINGER, R., *Adaptation of Higher Fungi to várzea conditions*. - *Amazoniana* 8: 311-319. 1984.
- SINGER, R. & I. ARAUJO, *Litter decomposition and ectomycorrhiza in Amazonian forests I*. *Acta Amazonica* 9: 25-41. 1979.
- SINGER, R., I. ARAUJO & M.H. IVORY, *Litter decomposition and ectomycorrhiza in Amazonian forests II. The ectotrophically mycorrhizal fungi of the neotropical forests...* *Nov. Hedw. Beih.* 77: 1-339, 19 plts. 1983.
- SINGER, R. & A. ARCHANGELSKY, *A petrified basidiomycete in Patagonia*. - *Am. Journ. Bot.* 45: 194-198. 1958.
- SINGER, R. & E.E. BOTH, *A new species of Gastroboletus and its phylogenetic significance*. - *Mycologia* 69: 59-72. 1977.
- SINGER, R. & H. CLÉMENÇON, *Notes on some leucosporous and rhodosporous European Agarics*. *Nova Hedwigia* 23: 305-352. 1972.
- SINGER, R. & A.P.L. DIGILIO, *Prodromo de la flora agaricina Argentina*. - *Lilloa* 25: 5-462. 1952. (publ. 1953).
- SINGER, R. & A.P.L. DIGILIO, *Las boletaceas de Sudamérica tropical*. - *Lilloa* 30: 141-164. 1960.
- SINGER, R. & I.J. GAMUNDI, *Paraphyses*. - *Taxon* 12: 147-150. 1963.
- SINGER, R. & L.D. GOMEZ, *The Basidiomycetes of Costa Rica III. The genus Phylloporus (Boletaceae)*. - *Brenesia* 22: 163-181. 1984.

- SINGER, R. & K. GRINLING, *Some Agaricales from the Congo*. - *Persoonia* 4: 355-377. 1967.
- SINGER, R. & J. KUTHAN, *Einige interessante europäische Hygrophoraceae*. - *Zeitschr. f. Pilzk.* 42: 5-14. 1976.
- SINGER, R. & J. KUTHAN, *Notes on Chroogomphus*. - *Česká Mykologie* 30: 81-89. 1976.
- SINGER, R. & J. KUTHAN, *Comparison of some lignicolous white-spored American agarics with European species*. - *Česká Mykologie* 34: 57-73. 1980.
- SINGER, R. & R.E. MACHOL, *Bayesian analysis of generic relations in Agaricales*. - *Nov. Hedw.* 21: 753-787. 1971.
- SINGER, R. & J.H. MORELLO, *Ectotrophic mycorrhiza and forest communities*. - *Ecology* 41: 549-551. 1960.
- SINGER, R. & M. MOSER, *Forest mycology and forest communities in South America I*. - *Mycopath. Myc. Appl.* 26: 129-191. 1965.
- SINGER, R. & B. SINGH, *Two new ectotroph-forming boletes from India*. - *Mycopath. Myc. Appl.* 43: 25-33. 1971.
- SINGER, R. & A.H. SMITH, *A monograph on the genus Leucopaxillus Boursier*. - *Pap. Mich. Acad. Sc. Arts Lett.* 28: 85-132, pl. 1-8. 1943.
- SINGER, R. & A.H. SMITH, *The taxonomic position of Pholiota mutabilis and related species*. - *Mycologia* 38: 500-523. 1946.
- SINGER, R. & A.H. SMITH, *Proposals concerning the nomenclature of the Gill fungi including a list of proposed lectotypes and genera conservanda*. - *Mycologia* 38: 240-299. 1946.
- SINGER, R. & A.H. SMITH, *Emendations to our proposals ...* - *Mycol.* 40: 627. 1948.
- SINGER, R. & A.H. SMITH, *Notes on secotiaceous fungi 1-9*. - *Brittonia* 10: 201-216. 1958; *Bull. Torr. Cl.* 85: 324-334. 1958; *Brittonia* 11: 205-223, 223-228. 1959; *Madroño* 15: 73-79; 52-158, 1959-1960; *Mycologia* 50: 927-938. 1959; *Mem. Torr. Bot. Cl.* 21: 1-112. 1960.
- SINGER, R. & A.H. SMITH, W.H. SNELL & W.L. WHITE, *The taxonomic position of Polyporoletus sublividus* *Mycologia* 37: 124-128. 1945.
- SMITH, A.H., *Investigations of two-spored forms in the genus Mycena*. - *Mycologia* 26: 305-331, pl. 34-38. 1934.
- SMITH, A.H., *Studies on the genus Cortinarius I*. - *Contrib. Univ. Mich.* 2: 5-42, pl. 1-11. 1939.
- SMITH, A.H., *Studies on the purple-brown-spored Agarics*. - *Mycologia* 31: 544-557. 1939.
- SMITH, A.H., *Notes on agarics from British Honduras*. - *Contrib. Univ. Mich. Herb.* 1: 21-28. 1939.
- SMITH, A.H., *Certain species of Inocybe in the herbarium ...* - *Pap. Mich. Acad. Sc. Arts Letters* 24: 93-106, pl. 1-6, 1939.
- SMITH, A.H., *Studies in the genus Agaricus*. - *Pap. Mich. Acad. Sci. Arts Lett.* 25: 107-138, pl. 1-10. 1939 [1940].
- SMITH, A.H., *New and unusual agarics from North America*. - I. *Mycologia* 30: 20-41. 1938; II. *ibid.* 33: 1-16. 1941.
- SMITH, A., *Studies on North American Agarics*. - *Contrib. Univ. Mich. Herb.* 5: 1-73, pl. 1-32. 1941.
- SMITH, A.H., *New and interesting Cortinarii from North America*. - *Lloydia* 7: 163-235. 1944.
- SMITH, A.H., *Unusual North American Agarics*. - *The Amer. Midl. Nat.* 32: 669-698. 1944.
- SMITH, A.H., *North American Species of Mycena*, pp. i-xviii, 1-521, pl. 1-99. Ann Arbor 1947. (Reprint Lehre 1969.)
- SMITH, A.H., *Mushrooms in their natural habitats I, I-XIX*, 1-626; II (Stereophorographs). Portland 1949.

- SMITH, A.H., *The North American species of Naematoloma*. - *Mycologia* 43: 467-521. 1951.
- SMITH, A.H., *New rare agarics ... and ... North American species of Xeromphalina*. - *Pap. Mich. Acad. Sc., Arts & Lett.* 38: 53-87. 1953.
- SMITH, A.H., *Additional new or unusual North American Agarics*. - *Sydowia Beih.* 1 (Festschr. f. Franz Petrak): 46-51. 1956.
- SMITH, A.H., *A contribution toward a monograph of Phaeocollybia*. - *Brittonia* 9: 195-217. 1957.
- SMITH, A.H., *Tricholomopsis (Agaricales) in the Western Hemisphere*. - *Brittonia* 12: 41-70. 1960.
- SMITH, A.H., *The hyphal structure of the basidiocarp* in Ainsworth, G.C., & A.S. Sussman, *The Fungi* 2: 151-177. 1966.
- SMITH, A.H., *The origin and evolution of the Agaricales* in R.H. Petersen (1971b), pp. 481-504.
- SMITH, A.H., *The North American species of Psathyrella*. - *Memoirs N. Y. Bot. Gard.* 24. 633 pp. 1972.
- SMITH, A.H. & H.J. BRODIE, *Cultural characters and pairing reactions of monosporous mycelia and development of the fruit body of Pholiota (Flammula) polychroa*. - *Bot. Gazette* 96: 533-546. 1935.
- SMITH, A.H., V.S. EVENSON & D.H. MITCHEL, *The veiled species of Hebeloma in the Western United States* - Ann Arbor 1983.
- SMITH, A.H. & L.R. HESLER, *New and unusual Agarics from the Great Smoky Mountains National Park*. - *Journ. Elisha Mitchell Sc. Soc.* 56: 302-324, pl. 7-12. 1940.
- SMITH, A.H. & L.R. HESLER, *Studies in the North American species of Hygrophorus*. - I. *Lloydia* 2: 1-62. 1939; *ibid.* II. 5: 1-94. 1942.
- SMITH, A.H. & L.R. HESLER, *Additional North American Hygrophori*. - *Sydowia* 8: 304-333. 1954.
- SMITH, A.H. & L.R. HESLER, *The North American species of Pholiota*. Hafner, 1-402. 1968.
- SMITH, A.H. & R. SINGER, *A monograph on the genus Cystoderma*. - *Pap. Mich. Acad. Sc. Arts Lett.* 30: 71-124, pp. 1-5. 1945.
- SMITH, A.H. & R. SINGER, *The genus Galerina*. - *Sydowia* 11: 446-453. 1957.
- SMITH, A.H. & R. SINGER, *A monograph on the genus Galerina Earle*. Hafner, pp. 1-384. 1964.
- SMITH, A.H. & H.D. THIERS, *A contribution toward a monograph of North American species of Suillus*. Ann. Arbor 1-116. 1964.
- SMITH, A.H. & H.D. THIERS, *The Boletes of Michigan*, pp. 1-417. 1971.
- SMITH, A.H. & H.D. THIERS & R. WATLING, *A preliminary account of the North American species of Leccinum...* *Mich. Bot.* 5: 131-179, 1966; 6: 107-154. 1967.
- SMITH, HELEN V., *The genus Limacella in North America*. - *Pap. Mich. Acad. Sc. Arts Lett.* 30: 125-147. 1944 [1945].
- SNELL, W.H., *The genera of Boletaceae*. - *Mycologia* 33: 415-423. 1941.
- SNELL, W.H., *New proposals relating to the genera of the Boletaceae*. - *Mycologia* 34: 403-411. 1942.
- SNELL, W.H. & E.A. DICK, *A glossary of mycology*, pp. 1-170. Cambridge, Mass. 1957.
- SNELL, W.H. & E.A. DICK, *The boleti of Eastern North America*. Lehre 1970.
- SNELL, W.H., R. SINGER & E.A. DICK, *Notes on boletes* 11. - *Mycologia* 51: 564-577. 1959 (publ. 1960).
- STALPERS, J.A., *Heterobasidion (Fomes) annosum and the Bondarzewiaceae*. - *Taxon* 28: 414-416. 1979.
- STANKOVICOVÁ, L., *Hyphal structure in some pleurotoid species of Agaricales*. - *Nov. Hedw.* 24: 61-120. 1973.

- STEGLICH, W., W. FURTNER & A. PROX, *Neue Pulvinsäurederivate aus Xerocomus chrysenteron (Bull. ex St. Amans) Quél.* - Zeitschr. f. Naturforschung 23b: 1044-1050. 1968.
- STEGLICH, W., W. FURTNER & A. PROX, *Xerocomssäure und Gomphidsäure....* Z. f. Naturforsch. 24b:(7). 1969.
- STEGLICH, W.W. FURTNER & A. PROX, *Variegatorubin, ein Oxydationsprodukt der Variegatsäure aus Suillus piperatus und anderen Boletaceen.* - Zeitschr. f. Naturforschung 25b: 557-558. 1970.
- STEGLICH, W., W. LÖSEL & V. AUSTEL, *Anthrachinon-Pigmente aus Dermocybe sanguinea (Wulf. ex Fr.) Wünsche und D. semisanguinea (Fr.).* Chem. Ber. 102: 4103-4118. 1969.
- STEGLICH, W., I. PILS & A. BRESINSKY, *Nachweis und chemotaxonomische Bewertung von Pulvin-säuren in Rhizopogon (Pigments of Fungi VIII).* - Z. Naturforsch. 26b: 376-377. 1971.
- STEGLICH, W., A. THILMANN, H. BESL & A. BRESENSKY, *2,5-Diarylcylopantan-1,3-dione aus Chamonixia caespitosa (Basidiomycetes) (Pilzpigmente 291).* - Z. Naturforsch 32c: 46-48. 1977.
- SVRČEK, M., *A revision of some genera of Agaricales described by J. Velenovsky.* Česka Mykologie 20: 69-74.
- TABER, W.A., *Morphogenesis in Basidiomycetes* in AINSWORTH, G.C., & A.S. SUSSMAN, *The Fungi II*, pp. 387-412. 1966.
- THIERS, H.D., *Some ideas concerning the phylogeny and evolution of the boletes.* In: Petersen (ed.), *Evolution of the Higher Basidiomycetes.* pp. 423-440. 1971.
- THOMPSON, G.E., *Nyctalis parasitica and N. asterophora in culture.* - Mycologia 28: 222-227. 1936.
- THORN, R.G. & G.L. BARRON, *Carnivorous mushrooms.* - Science 224: 76-78. 1984.
- TRESCHOW, C., *Nutrition of the cultivated mushroom.* - Dansk Bot. Ark. 11 (6). 1944.
- TYLER JR., V.E., *Chemotaxonomy in the higher Basidiomycetes* in R.H. PETERSEN (1971b), pp. 29-62.
- TYLER, V.E., R.G. BENEDICT & D.E. STUNTZ, *Chemotaxonomic significance of the ucea in higher fungi.* - Lloydia 28: 342-353. 1965.
- ULBRICH, E., *Bildungsabweichungen bei Hutpilzen.* Berlin-Dahlem 1-104. 1926.
- VANDENDRIES, R., *Recherches sur la sexualité des Basidiomycètes.* - C. r. Soc. Biol. 86: 513. 1922.
- VANDENDRIES, R., *Recherches sur le déterminism sexuel des Basidiomycètes.* - Mém. Ac. R. Belgique 1923.
- VANDENDRIES, R., *Contribution nouvelle à l'étude de la sexualité des Basidiomycètes.* - La Cellule. 35: 129-155. 1924.
- VANDENDRIES, R., *Recherches expérimentales prouvant la fixité du sexe dans Coprinus radians.* Desm. - Bull. Soc. Myc. Fr. 41: 358-374. 1925.
- VANDENDRIES, R., *Les mutations sexuelles. L'hétéro-homothallism et la stérilité entre races géographiques de Coprinus micaceus.* - Mém. Acad. R. Belg. 9: 1-50. 1927.
- VANDENDRIES, R., *La tétrapolarité et les mutations sexuelles chez Hypholoma hydrophilum.* - Bull. Soc. R. Bot. Belg. 63: 26-35. 1930.
- VANDENDRIES, R., *Les aptitudes et les mutations sexuelles chez Panaeolus papilionaceus Fr.* - Rec. Trav. déd. L. Mangin, pp. 31-39. Paris 1931.
- VANDENDRIES, R., *Tetrapolarité sexuelle de Pleurotus columbinus.* - Cellule 41: 265. 1934.
- VANDENDRIES, R., *De la valeur du barrage sexuel .... Pleurotus ostreatus.* - Genetica 15: 202-212. 1933.
- VANDENDRIES, R., *La polarité sexuelle et le régime conidien chez Pleurotus pinsitus.* - Bull. Soc. Myc. Fr. 50: 203-212. 1934.

- VANDENDRIËS, R., *Nouveaux aperçus sur la sexualité des Basidiomycètes*. - Comp. r. Acad. Sc. 204: 1084. 1937.
- VANDENDRIES, R., *Modalités sexuelles des Basidiomycètes*. - Bull. Soc. R. Bot. Belg. 20: 66-85. 1937.
- VANDENDRIES, R. & H.J. BRODIE, *Étude expérimentale des barrages sexuels*. - La Cellule 12: 160-210. 1933.
- VASILKOV, B.P., *Tri význačné druhy kloboukatých hub na bylinách*. - Česká Mikologie 15: 31-35. 1961.
- WAGER, H.W.F., *On nuclear division of the Hymenomycetes*. - Ann. Bot. 7: 489-514, pl. 24-26. 1893.
- WAKAYAMA, K., *Contribution to the cytology of fungi*. - I. Cytologia 1: 369-388. 1930; IV. Cytologia 3: 260. 1933.
- WALKER, L.B., *The development of Pluteus admirabilis and Tubaria furfuracea*. - Bot. Gaz. 68: 1-21. 1919.
- WATLING, R., *The genus Paragyrodon*. Not. R. bot. Gard. 29: 67-73. 1969.
- WATLING, R. *Boletaceae: Gomphidiaceae: Paxillaceae*. In: Henderson & al. (eds.). *British flora*. Edinburgh. 1970.
- WATLING, R., *Polymorphism in Psilocybe merdaria*. - New Phytol. 70: 307-336. 1971.
- WATLING, R., *Bolbitiaceae*. In: Henderson, Orton & Watling (eds.) *British Fungus Flora* 3. Edinburgh 1982.
- WELLS, K. & E.K. WELLS, *Basidium and basidiocarp*. New York 1982.
- WESSELS, J.G.H., *Morphogenesis and biochemical processes in Schizophyllum commune Fr.* Wentia 13: 1-113. 1965.
- WIELAND, T., *Poisonous principles of mushrooms of the genus Amanita*. - Science 159: 946-952. 1968.
- WIELAND, T., G. LÜBEN, H. OTTENHEIM, J. FAESEL, J.X. DE VRIES, W. KONZ, A. PROX & J. SCHMIDT, *Antamanid, seine Entdeckung. Isolierung, Strukturaufklärung und Synthese*. - Angew. Chemie 80: 209-213. 1968.
- WOLFE, C.B., JR., *Austroboletus and Tylopilus subg. Porphyrellus*. - Biblioth. Myc. 69: 1-148. 1979.
- WOLFE, C.B., JR., *Mucilopilus a new genus of the Boletaceae* Mycotaxon 10: 116-132. 1979.
- WOLFE, C.B. & R.H. PETERSEN, *Taxonomy and nomenclature of the supraspecific taxa of Porphyrellus*. - Mycotaxon 7: 152-162. 1978.
- YATES, H.S., *A comparative histology of certain Californian Boletaceae*. - Univ. Calif. Publ. Bot. 6 (10): 221-247, pl. 21-25. 1916.
- ZELLER, S.M., *The development of the carpophores of Ceriomyces Zelleri*. - Mycologia 6: 235-239. 1914.
- ZELLER, S.M., *The development of Stropharia ambigua*. - Mycologia 6: 139-145. 1914.
- ZELLER, S.M., *New and noteworthy Gasteromycetes*. - Mycologia 33: 196-214. 1941.
- ZELLER, S.M., *North American species of Galeropsis, Gyrophragmium, Longia, and Montagnea*. - Mycologia 35: 409-321. 1943.
- ZEROVA, M.Y., P.E. SOSIN & G.L. ROJENKO, *Biznachnik gribyv Ukrainsk*. - V.2. Kiiv 1979.

## EXPLANATION OF THE PLATES

- Pl. 1. Fig. 1. *Gymnopilus aculeatus* on mycorrhiza-bearing rhizome of *Cattleya* sp. (epiphytic orchid), in a greenhouse at Harvard University, Cambridge Mass. Origin: Mexico.  
Fig. 2. *Gyrodon exiguus*. Strongly pleurotoid fresh carpophores from Mexico (phot. T. Herrera).
- Pl. 2. *Geopeltum carbonarium*. Fig. 1. Metuloids in Melzer reagent (pseudoamyloid),  $\times 250$ .  
Fig. 2. Metuloid in toluidin blue (metachromatic),  $\times 900$ .
- Pl. 3. *Crepidotus mollis*. Gelatinous upper layer contrasted with non-gelatinized lower layer of the trama of the pileus (the brown surface layer and the bluish cells floating above are spores), about  $\times 175$  (phot. Cléménçon & Singer).
- Pl. 4. *Pleurotus tuber-regium*, carpophores on Pachyma-type sclerotium,  $\times 0.75$ .
- Pl. 5. *Panus fulvus*, carpophores on pseudosclerotium,  $\times 1$ .
- Pl. 6. *Melanotus ?musaecola*, carpophores damaging fabric in the tropics (Panamá Canal Zone), fruiting on this gray duck (exposed) which was damaged by the mycelium,  $\times 1.2$ .
- Pl. 7. *Entoloma abortivum* (*Acurtis giganteus*), both agaricoid carpophores and carpophoroids in their natural habitat,  $\times 0.8$ .
- Pl. 8. *Lampteromyces japonicus*, fresh specimens, in Fig. 1 seen in absolute darkness; while the background is darkened out, the carpophores are luminescent enough to show on the film.  
Fig. 2. Same group of carpophores in daylight seen from below (showing the veil). Fig. 3. Carpophores seen from above, in daylight.
- Pl. 9. *Calocybe cyanella*, basidia, with carminophilous granulosity (acetocarmine, oil immersion),  $\times 1700$ .
- Pl. 10. *Clitopilus prunulus*, spores in frontal view (fusoid), in profile (inequilaterally fusiform), and in polar view (see from one of the tips with the longitudinal axis vertical, here seen as angular to substellate bodies), oil immersion,  $\times 780$ .
- Pl. 11. *Asterophora lycoperdoides*, chlamydospores,  $\times 560$ .
- Pl. 12. Fig. 1. *Entoloma squamifolium*, spores, angular, of the axially symmetric type, strongly enlarged,  $\times 3750$ .  
Fig. 2. *Galerina evelata*, spores of the calyptate type,  $\times 4000$ .
- Pl. 13. *Psilocybe montana*, spores, of the lenticiform type, with germ pore. The narrow spores are seen in profile, the broadest ones in frontal view; two spores in intermediate position,  $\times 4900$ .
- Pl. 14. Fig. 1. *Russula puiggarii*, spores in the Melzter reagent whereby the exospore ornamentation shows blackish violet on subhyaline ground, revealing an ornamentation of the type I (reticulate); almost perfectly round spores, in spite of the oblique hilar appendage, seem almost orthotropic,  $\times 1550$ .  
Fig. 2. *Porphyrellus subflavidus*, spores with heterogeneous wall, ornamentation of type XI,  $\times 2000$ .  
Fig. 3. Same,  $\times 900$ .
- Pl. 15. *Galerina marginata*, spores with plage (showing as round white spot in those spores which have their inner side turned towards the objective), oil immersion,  $\times 1100$ .
- Pl. 16. *Entoloma squamifolium*, spores scattered on the hymenium (round bodies are basidia seen from above), showing in frontal view a nearly right angled basal (hilar) end; other spores seen in profile; spores with axial symmetry, angular,  $\times 1230$ .
- Pl. 17. *Inocybe paludinella*, spores with low rounded tubercular processes as often found in subgenus *Inocybe*; also three metuloids,  $\times 1820$ .
- Pl. 18. *Inocybe paludinella*, muricate thick-walled metuloids of the *Inocybe*-type; also one spore,  $\times 2050$ .
- Pl. 19. *Hohenbuehelia angustata*, hymenium with metuloid (deep-rooting and thick-walled),  $\times 1520$ .
- Pl. 20. *Tubosaeta brunneosetosa*, brownish setoid cystidia,  $\times 1360$ , also one spore, typical for the Boletaceae.

- Pl. 21. Fig. 1. *Conocybe rickenii*, cheilocystidium,  $\times 1820$ .  
 Fig. 2. *Pluteus atricapillus*, metuloid with prongs, *Cervinus*-type,  $\times 1050$ .  
 Fig. 3. *Lactocollybia cycadicola*, gloeocystidium in cresyl blue mount (deep blue in preparation),  $\times 850$ .  
 Fig. 4. *Russula schiffneri*, macrocystidium (projecting to the upper left) among basidia and basidioles,  $\times 1000$ .  
 Fig. 5. *Melanoleuca* sp., cystidiole of one of the types characteristic for *Melanoleuca*, in cresyl blue mount, its wall purplish in the preparation; basidia (here black) are deep violet in the preparation,  $\times 1225$ .
- Pl. 22. *Stropharia aeruginosa*, chrysocystidia in cotton blue mount (the internal body appearing yellow in KOH has turned deep blue-black in the preparation),  $\times 1000$ .
- Pl. 23. *Coprinus micaceus*, section of the lamellae which are not wedge shaped (but compare Pl. 27, Fig. 1); note the vesiculose cystidia (trabecular cystidia) on the left hymenium of the second (from the left) lamella and on other points of the hymenia (some have been torn loose by the separating lamellae 1 and 2 and are floating in the medium),  $\times 155$ .
- Pl. 24. Fig. 1. *Panis rufus* var. *strigellus*, section of the lamella (edge towards right lower corner), showing completely irregular structure of the hymenophoral trama and absence of a subhymenium although section was treated with dyes exactly like Pl. 26, Fig. 4 (*Pleurotus*).  
 Fig. 2. *Coprinus ebulbosus*, section of the upper portion of a lamellae showing the pavement-like arrangement of the pseudoparaphyses which are optically "empty", i.e. almost devoid of protoplasm, while the basidia take on the phloxine-KOH and stand out among the pseudoparaphyses; the basidia of two sizes, one equalling the pseudoparaphyses, the other projecting (see right side hymenium) beyond them; note the thinness of the hymenophoral trama; dark spots are spores (two of them showing truncate germ pore),  $\times 175$ .
- Pl. 25. *Boletus russellii*, section through the young hymenophore, showing the bilateral hymenophoral trama, *Boletus*-type, the mediostratum in the middle of the tube wall is darker colored (though unstained), the lateral trama divergent; the pores are in the direction of the lower right corner. Leitz dry objective,  $\times 575$ .
- Pl. 26. *Chamaeota sphaerospora*, section through the lamellae showing the inverse hymenophoral trama; the edge of the lamella is in the direction of the lower right corner; hyphae of trama divergent but inversely as compared with Pl. 24,  $\times 850$ .
- Pl. 27. Fig. 1. *Lactarius volemus* var. *corrugis*, section through the carpophore in tangential direction, near the margin of the pileus. Innumerable dermatocystidia form the palisade of the cuticular layer of the pileus; numerous laticiferous vessels in the trama of the pileus (dark wormlike bodies in context); numerous cystidia in the hymenium along the lamellae which, in section, show the characteristic wedge-shape of the majority of the agarics; trama of the lamellae almost regular (not intermixed),  $\times 50$ .  
 Fig. 2. *Conocybe rickenii*, section through the lamella, showing the voluminous cells of the hymenopodium of each corresponding side of the lamella almost touching each other, with the trama proper (fine filamentous hyphae) between them strongly reduced,  $\times 270$ .  
 Fig. 3. *Hygrocybe cuspidata*, section through lamella, showing the strictly regular structure of the hymenophoral trama in sect. *Hygrocybe*; the hymenium on the left side partly broken off,  $\times 200$ .  
 Fig. 4. *Pleurotus levis*, section through lamella (with the edge beyond the upper margin of the figure), showing irregular trama with the characteristic well developed subhymenium of the genus *Pleurotus* (white zone immediately below the dark outer zone formed by the hymenia); section was first treated with KOH, then naturalized, then first dyed with phloxine which, for contrast, is replaced by cotton blue in the trama and the hymenium, thus the subhymenium remaining pink while the hymenium and the trama proper (as far inwards as the cotton blue penetrated) are blue; the blue zones appear darker than the pink zones (yellow filter is used to accentuate contrast),  $\times 90$ .
- Pl. 28. *Phylloporopsis nidulans*, hyphae forming the tomentum of the pileus, showing clamp connections, oil immersion,  $\times 1450$ .
- Pl. 29. *Russula tenuiceps*, intermixed (heteromerous) trama, the spherocysts predominant, but some fine filamentous connective hyphae also visible; section of stipe tissue,  $\times 1100$ .

- Pl. 30. *Hohenbuehelia angustata*. Gelatinous layer, consisting of loosely arranged hyphae imbedded in a gelatinous mass (light zone); above it the cuticular layer (which is of the "dense" type), facing the left upper corner, beneath (lower right half of the figure) the nongelatinized portion of the trama of the pileus,  $\times 550$ .
- Pl. 31. *Linderomyces lateritius*, coscinoid, first treated with KOH, then dyed with phloxine; oil immersion,  $\times 2400$ .
- Pl. 32. *Marasmius haematocephalus*, hymeniform layer of the broom cells (*Siccus*-type), *Marasmius*-cystidia showing below in the hymenium,  $\times 1050$ .
- Pl. 33. Fig. 1. *Amanita inaurata*, section of the covering of the pileus, the upper, darker zone is the volval layer of the young carpophore consisting of a relatively large number of spherocysts and some connective hyphae; cuticle proper somewhat gelatinized and hyphae loosely arranged; beneath the cuticle proper an oleiferous hypha dyed with phloxine (KOH),  $\times 750$ .  
 Fig. 2. *Lactocollybia cycadicola*, gloeo-vessel in the trama. On the slightly colored back-ground of ordinary hyphae, the gloeo-vessel appears almost black (deep blue in cresyl blue), oil immersion,  $\times 1620$ .
- Pl. 34. *Lactarius nigroviolescens*, cuticle, showing the *Virescens*-structure characteristic for sect. *Plinthogali*; this structure consists of spherocysts which are dark (pigmented!) and from them, one observes, arise ciliate dermatocystidia which form the surface of the cuticular layer; underneath, in the trama of the pileus, conspicuous filamentous tubes are visible, the laticiferous vessels, often with some contents, and more refringent than other tromal elements,  $\times 650$ .
- Pl. 35. *Cystoderma fallax*, epithelium, consisting of isodiametric cells (spherocysts) superimposed over hyphae of the pileus trama (which are hyaline in KOH, left lower part of photograph); the dark color of the epithelium is caused by the color reaction characteristic for several *Cystoderma* spec. which is observed in the cuticular layer whereby KOH (used as medium in this section) turns it very dark rusty cinnamon,  $\times 450$ .
- Pl. 36. *Entoloma squamifolium*, hair-like ornament of the pileus, consisting of several elongated cells in parallel arrangement,  $\times 750$ .
- Pl. 37. *Resupinatus dealbatus*, showing the asterostromelloid structure (a dichophysoid photograph) above the loosely hyphous trama of the pileus below. To show the fine structure of the cuticular layer, the section had to be brutally compressed and partly disrupted, oil immersion,  $\times 1850$ .
- Pl. 38. *Mycena dissimilabilis*, section through the cuticle and underlying trama showing the epicutis of thin-filamentous hyphae with the outermost hyphae diverticulate in the typical *Mycena*-manner; more voluminous hyphae are seen in the pigmented hypodermium below, also characteristic for many *Mycenae*, oil immersion,  $\times 920$ .
- Pl. 39. *Russula tenuiceps*, section through the cuticle of the pileus, showing numerous dermatocystidia of the macrocystidial type with banded-granular (yellow in ammonia) contents, oil immersion,  $\times 1550$ .
- Pl. 40. *Leccinum snellii*, section through the fascicles of hymenium covering the scales of the stipe characteristic for the genus; this extrahymenoporal hymenium consists of dermatopseudopara-physes (one plainly visible: broad cells in lower right corner pointing left), dermatobasidia (one bearing sterigmata visible in the center), and dermatocystidia (an ampullaceous body in right upper corner!); the basidiomorphous clavate bodies without sterigmata are either basidioles or undifferentiated cystidioles,  $\times 1120$ .
- Pl. 41. *Mycena osmundicola*, longitudinal section through the outer layer of the stipe. Long loose hairs, diverticulate all over, form the pubescent covering of the stipe. Aceto-carmine mount, oil immersion,  $\times 1160$ .
- Pl. 42. Above: *Agrocybe aegerita*, carpophore, showing (left) lamellae and inner side of annulus and (right section through carpophore,  $\times 1$ ).  
 Below: *Xerotinus afer*, carpophore from below (typus),  $\times 1$ .
- Pl. 43. *Arthrosorella ditopa*, showing two agaricoid carpophores (with clitocyboid habit) and, between them, five arthrosorocarps (*Nothoclavulina*-stage).
- Pl. 44. Above: *Shorea robusta* short roots, associated with *Pulveroboletus* and *Xerocomus* (ectomycorrhiza of Dipterocarpaceae, phot. B. Singh).  
 Below: *Phaeocollybia columbiana*, carpophores with georrhiza, fresh, typus,  $\times 0.6$ .

- Pl. 45-52 Spore replicas seen under the scanning microscope (electron micrographs by Pegler & Young)**
- Pl. 45. Lyophylleae (Tricholomataceae).
- Fig. 1. *Lyophyllum decastes*,  $\times 7000$ .
- Fig. 2. *Hypszigys ulmarius*,  $\times 1750$ .
- Fig. 3. *Calocybe gambosa*,  $\times 7000$ .
- Fig. 4. *Lyophyllum sphaerosporum*,  $\times 9800$ .
- Fig. 5. Same, showing open-pore hilum,  $\times 49000$  (electron-micrographs by Pegler & Young).
- Pl. 46. Spore replicas seen under the scanning microscope: Spores of Tricholomataceae.**
- Fig. 1. *Laccaria laccata*,  $\times 6500$  (scanning micrograph).
- Fig. 2. *L. amethystina*, 5600 (replica).
- Fig. 3. *L. laccata*,  $\times 13000$  (scanning micrograph of the spines).
- Fig. 4. *Asterophora parasitica*,  $\times 7000$  (replica).
- Fig. 5. *Clitocybe vibecina*,  $\times 7000$  (replica).
- Fig. 6. *C. clavipes*,  $\times 7000$  (replica).
- Fig. 7. Same,  $\times 1750$  (replica).
- Pl. 47. Spores (replicas excepting Fig. 2 which is a scanning micrograph) of various Tricholomataceae and Paxillaceae.**
- Fig. 1. *Ripartites tricholoma*,  $\times 17500$ , adaxial view.
- Fig. 2. *Lepista nuda*,  $\times 5900$ .
- Fig. 3. *Armillariella mellea* (or related form),  $\times 1750$ .
- Fig. 4. *Ripartites tricholoma*,  $\times 7000$ , abaxial view.
- Fig. 5. *Lepista personata*,  $\times 7000$ , adaxial view.
- Fig. 6. *Lepista gilva*,  $\times 7000$ , abaxial view.
- Fig. 7. Same, lateral view.
- Fig. 8. *L. sordida*,  $\times 8000$ , adaxial view (with nodulose hilum).
- Pl. 48. Spore replicas seen under the scanning microscope: Spores of Tricholomataceae.**
- Fig. 1. *Baeospora myosura*  $\times 11500$ .
- Fig. 2. *Flammulina velutipes*,  $\times 17500$  (the hilar appendage appressed to the spore).
- Fig. 3. *Collybia peronata*,  $\times 1750$ .
- Fig. 4. *C. maculata*,  $\times 17000$ , lateral view of rugulose suprahilar region.
- Fig. 5. Same, adaxial view,  $\times 8600$ .
- Pl. 49. Spore replicas of *Oudemansiella*-spores under the scanning microscope.**
- Fig. 1. *O. radicata*,  $\times 4375$ , lateral view.
- Fig. 2. Same,  $\times 4375$ , adaxial view.
- Fig. 3. *O. canarii*,  $\times 19600$ , showing rod-like wall projections.
- Fig. 4. Same,  $\times 17500$ , surface view.
- Fig. 5. Same,  $\times 2400$ .
- Fig. 6. *O. mucida*,  $\times 7000$ .
- Fig. 7. *O. radicata*,  $\times 7000$  (showing spore wall-ornament).
- Pl. 50. Spore replicas of Mycenae (Tricholomataceae) seen under the scanning microscope.**
- Fig. 1. *Mycena flavoalba*,  $\times 17500$ .
- Fig. 2. *M. galopoda*,  $\times 7000$ .
- Fig. 3. *M. epipytergia*, 6600.
- Fig. 4. *Fayodia bisphaerigera*,  $\times 4600$ , the perisprium (top layer of an excavated epitunica in Cléménçon's terminology) covering the underlying reticulate exosprium.
- Fig. 5. *Mycena haematopoda*,  $\times 5000$  (the groove probably due to distortion of the spore wall on landing).
- Pl. 51. Spore replicas of various Cortinariaceae and of *Phaeolepiota* (Agaricaceae) as seen under the scanning microscope.**
- Fig. 1. *Galerina hypnorum*,  $\times 9500$ .
- Fig. 2. *G. paludosa*,  $\times 3200$ , adaxial view.
- Fig. 3. Same,  $\times 3200$ , abaxial view.
- Fig. 4. *Phaeolepiota aurea*,  $\times 4200$ , abaxial view.
- Fig. 5. Same, adaxial view.
- Fig. 6. *Galerina paludosa*,  $\times 3200$ .
- Fig. 7/8. *G. tibiacytis*,  $\times 3600$ .

Pl. 52. Spore replicas as seen under the scanning microscope: Boletaceae.

Fig. 1. *Xerocomus subtomentosus*,  $\times 4600$ .

Fig. 2. *X. chrysenteron*,  $\times 4600$ .

Fig. 3. *Boletus erythropus*,  $\times 3600$ .

Fig. 4. *Xerocomus subtomentosus*.

Fig. 5. *Boletus pulverulentus*,  $\times 3200$ .

Fig. 6. *Leccinum scabrum*,  $\times 4200$ .

Fig. 7. *Chalciporus rubinus*,  $\times 7000$ .

Fig. 8. *Xerocomus subtomentosus*,  $\times 19600$ , spore base region.

Fig. 9. Same,  $\times 1750$ .

Pl. 53. Spore wall cross sections (EM,  $\times 50000$ ).

Fig. A. *Entoloma incanum*, corium (white inner layer), epicorium (spongy middle layer), and tunica (black outer layer). (Phot. Cléménçon).

Fig. B. *Oudemansiella mucida*.

Fig. C. *Cortinarius violaceus* (starting from below) a colored multilayered coriotunica covered by an epitunica (consisting of podostratum (thin, pale continuous layer just above the dark zone of the coriotunica), cerostratum (gray bulk-mass of the epitunica) and the dark mocostratum. (Phot. Cléménçon).

Pl. 54. Spore wall cross section (EM,  $\times 50000$ ) of *Lactarius griseus*. The coriotunica consists of an inner bright and an outer dark layer. An irregular tectum covers the coriotunica and forms the ornamentation. The tectum is covered by the black interstratum. The sporothecium consists of two layers, an inner, bright endosporothecium, and an outer, dark and floccose ectosporothecium (Phot. Cléménçon).

Pl. 55. EM section of spore of *Oudemansiella radicata*,  $\times 30000$ , the coriotunica and the ornamentals, the former corresponding to pl. 53, fig. B, the latter corresponding to pl. 49, fig. 7 (Phot. Pegler).

Pl. 56. *Fayodia deusta*.

Fig. 1. Phaecystidium with granular refractive contents, in KOH,  $\times 2000$ .

Fig. 2. Mature coelosphaerites of a phaecystidium,  $\times 50000$  (EM section) (Phot. Cléménçon).

Pl. 57. Above: *Campanella dendrophora*, sp = mature spores,  $\times 1100$ ; spg = germinating spores,  $\times 1100$ ; d = dendrophysoid elements,  $\times 760$ ; dc = dendrophysoid cystidia,  $\times 750$ ; cy = cystidia with subcapitate apex,  $\times 750$ ; met = metuloids,  $\times 750$ ; ca = carpophore,  $\times \frac{1}{2}$ ; b = basidium,  $\times 750$ . - Right center: *Panellus mirabilis*, dc = dermatocystidium,  $\times 1000$ ; d = diverticulate hyphal element of the epicutis of the pileus. - Below: *Pleurotus concavus* ca = carpophores, showing characteristic habit (clitocyboid) with common squamose base,  $\times 1$ ; h = fragment of the hymenium with hymenophoral trama underneath the basidia,  $\times 500$ ; sp = spore,  $\times 2000$ .

Pl. 58. Fig. 1. *Hydropus aristoteliae*, ch = cheilocystidia; sp = spore; pl = pleurocystidium; app = appendage of cheilocystidium, dc = dermatocystidium, all  $\times 2000$ .

Fig. 2. *Marasmiellus alliodorus*, ep = cells of epicutis of pileus, with (below) a medallion clamp; ch = four cheilocystidia to the right below the spore, and one to the left of the spore; sp = germinating spore; st = cell of the covering of the stipe, all  $\times 2000$ .

Pl. 59. Fig. 1. *Marasmius platyspermus*, epi = epicuticular broom cells of the pileus, *Rotalis*-type; sp = spore, all  $\times 1000$ .

Fig. 2. *Marasmius rotalis*, Ceylon, epicuticular broom cells, *Rotalis*-type,  $\times 1000$ .

Fig. 3. *Marasmius aff. rotalis*, Argentina, epicuticular broom cell,  $\times 1000$ .

Fig. 4. *Marasmius trichorhizus*, sp = spore,  $\times 1000$ .

Fig. 5. *Marasmius defibulatus*, sp = spore; epi = cheilocystidium (*Rotalis*-type) all  $\times 1000$ .

Fig. 6. *Marasmius nigrobrunneus*, epi = epicuticular broom cell of the *Siccus*-type,  $\times 1000$ .

Fig. 7. *Marasmius graminum* var. *cynodontis*, carpophores in natural size.

Fig. 8. *Marasmius graminum* var. *brevisporus*, sp = spores; epi = epicuticular broom cell of the *Siccus*-type,  $\times 1000$ .

Pl. 60. Fig. 1. *Marasmius ferrugineus*, sp = spores, one with two septa; chcy = broom cells from the edge of the lamellae; cy = pleurocystidium, all  $\times 1000$ .

Fig. 2. *Marasmius montagnei*, type, epi = epicuticular broom cell of the *Siccus*-type; cy = pleurocystidia, all  $\times 1000$ .

Fig. 3. *Marasmius anomalus*, type, cy = pleurocystidium,  $\times 1000$ .

Fig. 4. *Marasmius melinocephalus*, epi = broom cells of the *Siccus*-type on epicutis of pileus,  $\times 1000$ .

Fig. 5. *Marasmius haematocephalus*, cy = pleurocystidia; sp = spores, both  $\times 1000$ .

Fig. 6. *Marasmius helvolus*, carp = carpophores of type collection,  $\times 1$ ; cyst = pleurocystidium,  $\times 1000$ .

Fig. 7. *Marasmius glaucopus*, type, epi = epicuticular broom cell of the *Siccus*-type,  $\times 1000$ .

Pl. 61. *Mycena triplotricha*, ch = cheilocystidium; ep = cells of the covering of the pileus; st = hairs of the covering of the stipe, all  $\times 2000$ .

Pl. 62. Fig. 1. *Mycena tenerima*, ch = cheilocystidium; st = hairs of the stipe, both  $\times 2000$ .

Fig. 2. *Mycena nothomyrciae*, sp = spores,  $\times 2000$ .

Fig. 3. *Mycena camptophylla*, ch = cheilocystidium; dc = dermatocystidia of the stipe,  $\times 2000$ .

Fig. 4. *Mycena dryopteris*, ca = carpophore,  $\times 12$ ; ch = cheilocystidium,  $\times 2000$ ; dc = dermatocystidia of the stipe,  $\times 2000$ .

Fig. 5. *Mycena discogena*, sp = spore,  $\times 2000$ .

Pl. 63. Fig. 1. Showing the hairs of the pileus of *Marasmius chrysochaetes* and six different species of the genus *Crinipellis*,  $\times 450$  (a = *C. stuparia*, with the base of the hair in connection with the hyphae of the hypotrichium, and the upper portion of a hair; b = *C. mirabilis*; c = *C. carecomoeis* var. *litseae*; d = *C. stipitaria*, two forked hairs from the margin of the pileus; e = *C. septotricha*; f = *C. excentrica*; g = *Marasmius chrysochaetes*, pseudoamyloid bodies of the epicutis of the pileus).

Fig. 2. Showing elements of the hymenium of *Crinipellis* spp.,  $\times 450$  (a = *C. carecomoeis* var. *litseae*; basidia, some of them deformed; b = same, basidiole; c = same, cheilocystidia; d = *C. excentrica*, hymenium on the sides of the lamellae; basidia and basidiole; e = *C. siparuna*, basidia; f = *C. minutula*, pleurocystidia; g = same, cheilocystidia).

Fig. 3. Showing spores of some species of *Crinipellis* and *Chaetocalathus*,  $\times 900$  (a = *Crinipellis sepiaria*; b = *C. dipterocarpis*; c = *C. zonata*; d = *C. campanella*; e = *C. mirabilis*; f = *C. carecomoeis* var. *litseae*; g = *C. hirticeps*; h = *Chaetocalathus carneleruber*; i = *Ch. pachtrichus*).

Fig. 4. Showing some characters of *Chaetocalathus pachytrichus*, and *Ch. carneleruber* carpophores,  $\times 2$ , rest  $\times 450$ ; a = carpophore of *Ch. pachytrichus*; b = hair of pileus of same; c = basidium of same; d = a simple and a forked cystidium of same; e = cystidia of same (Tonkin material); f = carpophore of *C. carneleruber*; g = outline of cystidium of same; g = optical section of cystidium of same; i = hairs of pileus of same.

Pl. 64 - 67. Anatomical details of *Gloiocephala*, *Manuripia*, *Epicnaphus*, and *Hymenogloea* (all spores  $\times 2000$ ; all other anatomical microscopical drawings  $\times 1000$ ).

Pl. 64. Fig. 1. *Gloiocephala inobasis*, hc = hymenial cystidia; b = basidium; sp = spores; ca = carpophore,  $\times 1$ .

Fig. 2. *Gloiocephala palmarum*, cec = epicuticular cells, cystidoid; hm = hair-like metuloids; b = basidia; bl = basidiole; hc = hymenial cystidium.

Pl. 65. Fig. 3. *Gloiocephala palmarum*, ec = epicuticular cells forming cortical layer; sp = spore; ca = carpophores,  $\times 1$  and  $\times 10$ .

Fig. 4. *Gloiocephala lamellosa*, h = hairs; sp = spore; dcy = dermatocystidia of pileus; ec = epicuticular cells; ca = carpophore,  $\times 10$ .

Fig. 5. *Gloiocephala longifimbriata*, sp = spore, ca = carpophores,  $\times 1$ ; st = surface layer of stipe (lh = long hairs).

Pl. 66. Fig. 6. *Gloiocephala longifimbriata* ec = epicuticular cells; h = hair; dc = dermatocystidia of pileus.

Fig. 7. *Gloiocephala epiphylla*, pc = dermatocystidia of pileus; ee = epicuticular elements; cc = dermatocystidia of stipe; ca = carpophore,  $\times 10$ .

Fig. 8. *Gloiocephala spathularia*, dcp = dermatocystidia of pileus; ec = epicuticular cells; hc = hymenial cystidium; dst = dermatocystidia of stipe; sp = spore.

Pl. 67. Fig. 9. *Manuripia bifida*, rh = rhizomorph; epi = element of epicutis; cah = carpophores, habit,  $\times 1$ ; ca = carpophore,  $\times 4$ .

Fig. 10. *Epicnaphus phalaropus*, ca. = carpophores,  $\times 1$  and  $\times 4$ ; epi = epicuticular broom cells; sp = spore.

Fig. 11. *Hymenogloea papyracea*, cay = young carpophore,  $\times 1$ ; cam = mature carpophore,  $\times 1$ ; b = basidium; sp = spore; epi = three epicuticular elements.

- Pl. 68. Fig. A. *Leucopaxillus*, figs. 1-6 = spores, 7 = cuticular hyphae (1 = *L. laterarius*; 2 = *L. cerealis*; 3 = *L. giganteus*; 4 = *L. tricolor*; 5 = *L. gentianeus*; 6 = *L. subzonalis*; 7 = *L. gentianeus f. gentianeus*), all approximately  $\times 1485$ .  
 Fig. B. *Kuehneromyces* and *Pleuroflammula* (1 = *K. depauperatus*, cheilocystidium; 2 = *K. mutabilis*, spore in approximately frontal view, outer black line showing the episporium, inner thin line representing the inner surface of the endosporium, and the inner surface of the outer black line is the outer surface of the endosporium touching the episporium; a broad germ pore at the apex,  $\times 2700$ ).  
 Fig. 3. Same, cheilocystidia; at the right, a cheilocystidium with a drop of mucilage are the apex,  $\times 1175$ .  
 Fig. 4. *Pleuroflammula dussii*, cheilocystidium,  $\times 1175$ .  
 Fig. 5. *Pleuroflammula dussii*, spore; the outer black line represents the episporium; the inner black line the bright and deep colored ring inside the episporium; germ pore extremely narrow,  $\times 2700$ .  
 Fig. 6. *Kuehneromyces rostratus*, cheilocystidia,  $\times 1175$ .  
 Fig. 7. *Kuehneromyces vernalis*, five cheilocystidia in the middle representing the common type I, these are flanked by cheilocystidia of type II,  $\times 1175$ .
- Pl. 69. Fig. 1. *Pluteus xylophilus*, me = metuloid (M, of the *Magnus*-type, C, of the *Cervinus*-type),  $\times 900$ ; ca = carpophores, showing the pluteoid habit,  $\times 0.9$ ; sp = spores,  $\times 1800$ ; ch = cheilocystidia of two types,  $\times 900$ .  
 Fig. 2. *Pluteus stephanobasis*, figures at left lower corner - carpophores, -0.9 (vb = volval belt, left of it the primordium); meM = metuloid of the *Magnus*-type,  $\times 900$ ; sp = spores,  $\times 1800$ ; ch = cheilocystidia of two types,  $\times 900$ ; meC = metuloid of the *Cervinus*-type,  $\times 900$ .
- Pl. 70. Upper portion: *Pluteus granularis*, c = pleurocystidia,  $\times 500$ ; s = spore,  $\times 1000$ ; e = zone of the terminal members of the hyphal chains forming the epicutis of the pileus,  $\times 500$ ; ch = aberrant cheilocystidia,  $\times 500$ ; d = dermatocystidia of the stipe,  $\times 500$ . - Lower portion: Fig. 1. *Pluteus seticeps*, structure of epicutis, showing both epicuticular spherocysts and (elongated) dermatocystidia,  $\times 500$ . - Fig. 2. *Pluteus burserae*, type, e = structure of the epicutis of the pileus, with an obpiriform cell and a dermatocystidium (Dc); d2 = another dermatocystidium; di = a cell intermediate between a dermatocystidium and an ordinary epicuticular spherocyst; ch = cheilocystidium; cy = pleurocystidium, all  $\times 500$ .
- Pl. 71. Fig. 1. *Pluteus beniensis*, ca = carpophore,  $\times 0.9$ ; ep = elements of epicutis of pileus,  $\times 900$ ; cy = cystidia,  $\times 900$ .  
 Fig. 2. *Pluteus riograndensis* var. *riograndensis*, ep = elements of epicutis of pileus,  $\times 200$ ; ca = carpophore,  $\times 0.9$ .  
 Fig. 3. *Pluteus hololeucus*, ch = cheilocystidia; pl = pleurocystidia; ep = elements of epicutis of pileus, all  $\times 900$ .
- o f Pl. 72. Figs. 1-4. *Volvolepiota albida* (1 = basidium,  $\times 1000$ ; 2 = spore,  $\times 2000$ ; 3 = detail of the apical portion of the spore,  $\times 2200$ ; 4 = carpophore in longitudinal section, showing movable annulus and volva, remote-free lamellae and volval rest on pileus,  $\times 1$ ).  
 Figs. 5-7. *Cystoagaricus strobilomyces* (5 = two spores with common perispore,  $\times 1000$ ; 6 = single spores,  $\times 1000$ ; 7 = carpophores,  $\times 1$ ).
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Figs. 6-7. *Suillus decipiens* (6 = immature; 7 = mature carpophore).

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Fig. 5. *Boletus subsolitarius*, fragment of the hymenial layer on the margin of the pileus.

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Pl. 78. Anatomical details of the Boletaceae and *Gastroboletus*, camera lucida drawings from material mounted in KOH-phloxine (basidia and cystidia) and either NH<sub>4</sub>OH or Melzer mounts (spores), oil immersion, approximately,  $\times 1050$ .

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Fig. 7. *Boletellus ananas*, spores, basidium.

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Fig. 10. *Boletellus linderi*, spores, basidium.

Pl. 79. Anatomical details of *Marasmius marasmoides* (collection Singer B 3628), showing (ca) two carpophore sections,  $\times 1$ , (sp) spore,  $\times 2000$ , (hy) two basidioboles and three basidia, (dc) dermatocystidia, left - of the pileus, right - of the stipe, and (me) four metuloid cystidia of the hymenium, all  $\times 1000$ .

Pl. 80. Fig. 1. *Fayodia tetrasporigera*, carpophore ( $\times 1$ ), spore ( $\times 4000$ ), basidium ( $\times 1000$ ). Typus.

Fig. 2. *Xeromphalina longispora* (collection Schmitz-Levecq 220), carpophore ( $\times 1$ ); cystidia, cheilocystidia and dermatocystidia (upper row,  $\times 1000$ ); detail of the epicutis (middle below,  $\times 1000$ ) and a hyphal swelling in the gelatinized zone of the cuticle of the pileus ( $\times 1000$ ), extreme right: A hair of the covering of the stipe,  $\times 1000$ .

Pl. 81. *Galerina aimara* (collections B 502, B 652 - typus and paratypus). Carpophores  $\times 1$ , section,  $\times 1.5$ ; tibiiform cheilocystidia,  $\times 1000$ , and spores,  $\times 2000$ .

Pl. 82. *Galerina hypsizygia* (collection Dennis 1700). Carpophores  $\times 1$ , cheilocystidia,  $\times 1000$ , spore,  $\times 2000$ , dermatocystidia of the stipe (st),  $\times 1000$ . T = from other collection (Singer B 507 from Bolivian Andes).

Pl. 83. Fig. 1. *Galerina uchumachiensis* (collection B 1470, typus). Carpophore,  $\times 1$ ; spores,  $\times 2000$ ; cheilocystidium,  $\times 1000$ .

Fig. 2. *Gymnopilus macrosporus* (collection B 1229, typus). Carpophore,  $\times 1$ ; spore,  $\times 2000$ ; three cystidia and one basidium,  $\times 1000$ .

Pl. 84. Fig. CA. *Hiatallopsis amara*, section through carpophore, showing remote-free lamellae.

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- Pl. 85. Fig. 1. Gymnocarpous primordium.  
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Plate 1



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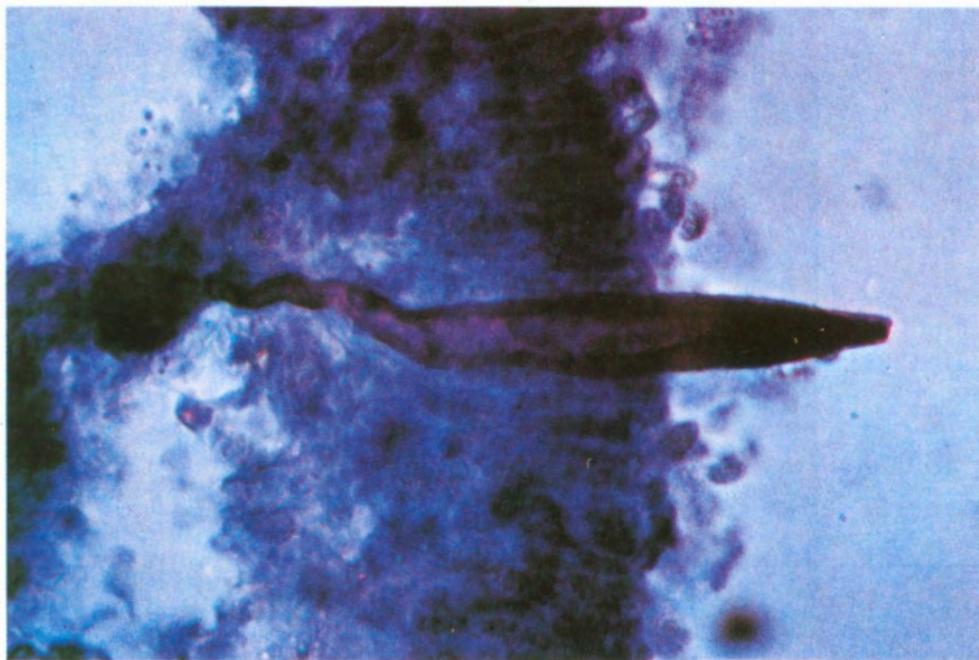


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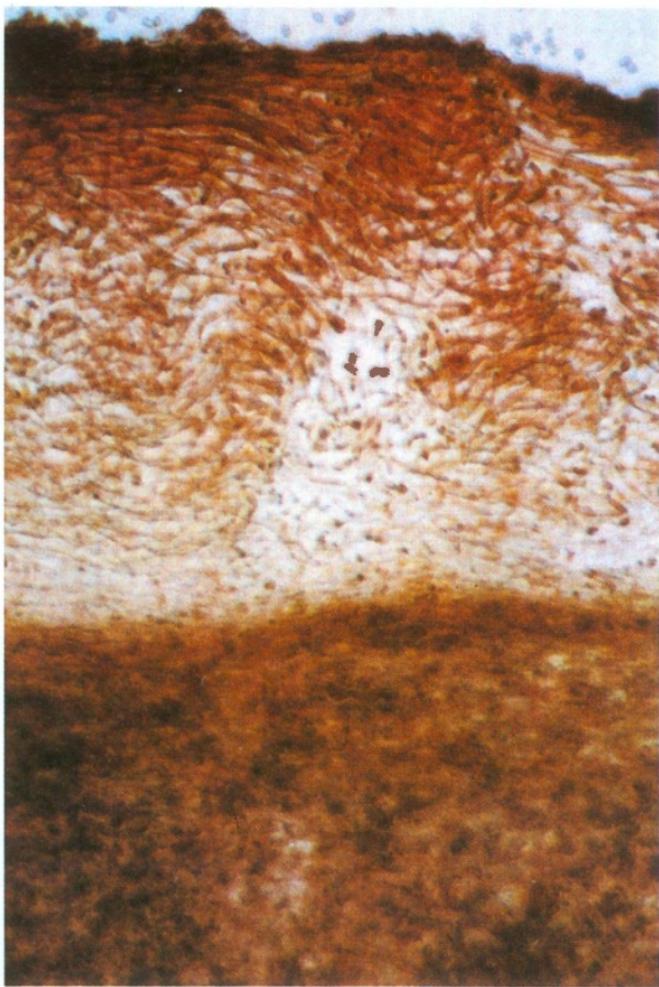
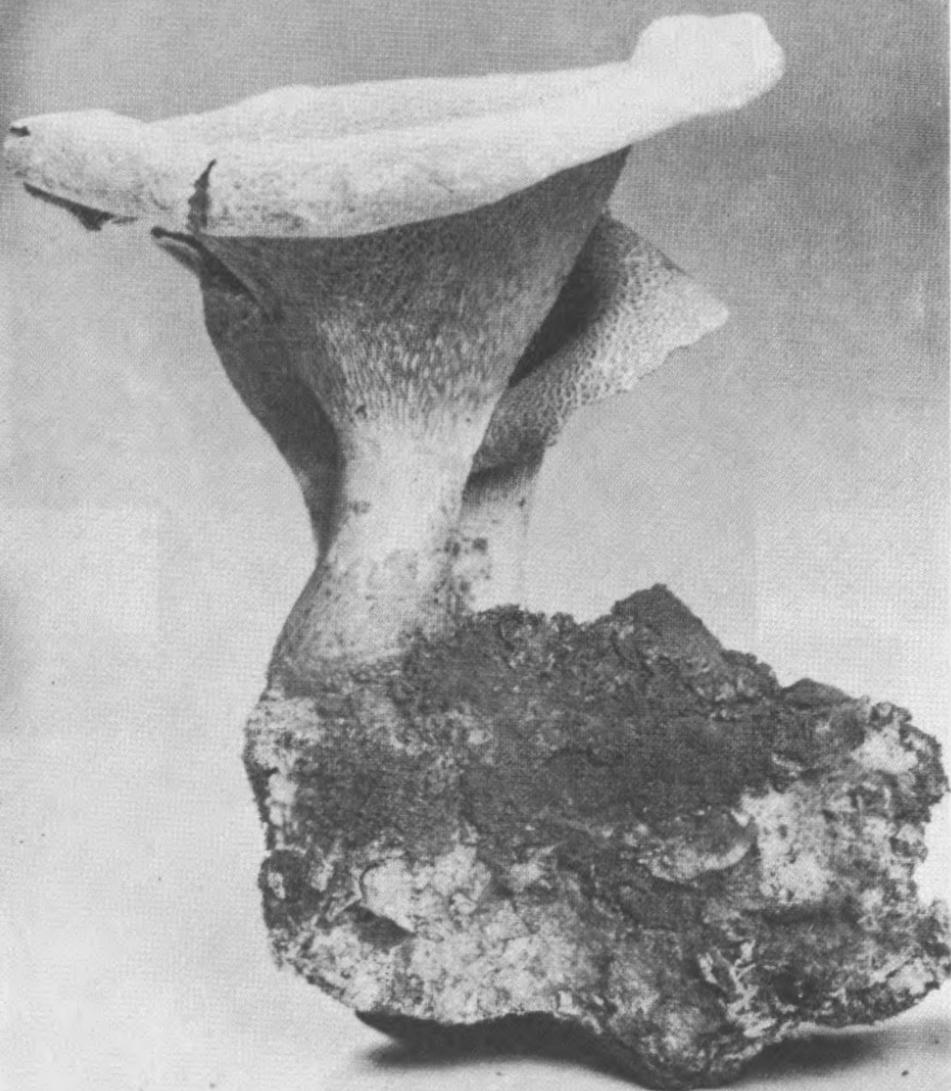


Plate 4



**Plate 5**

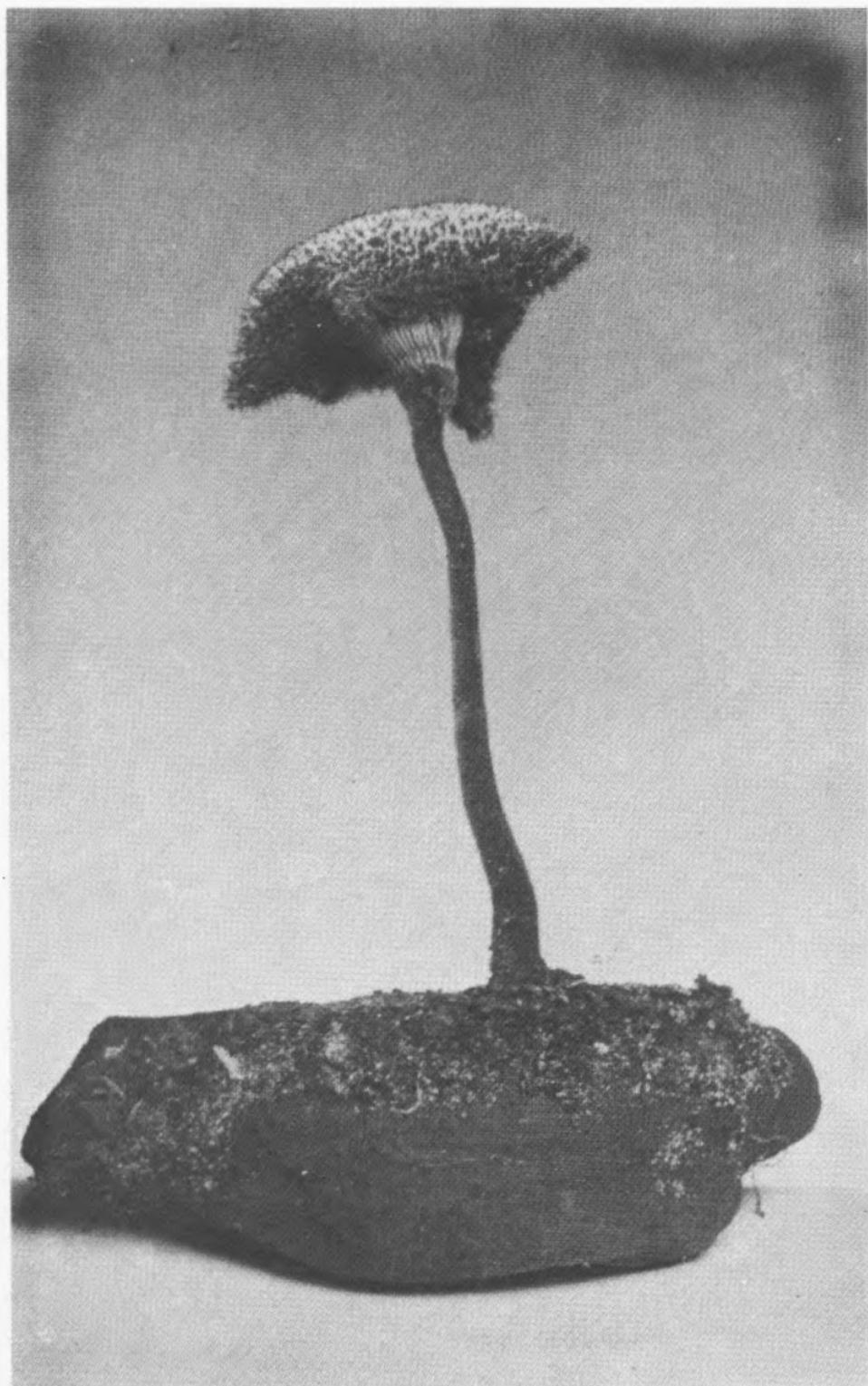


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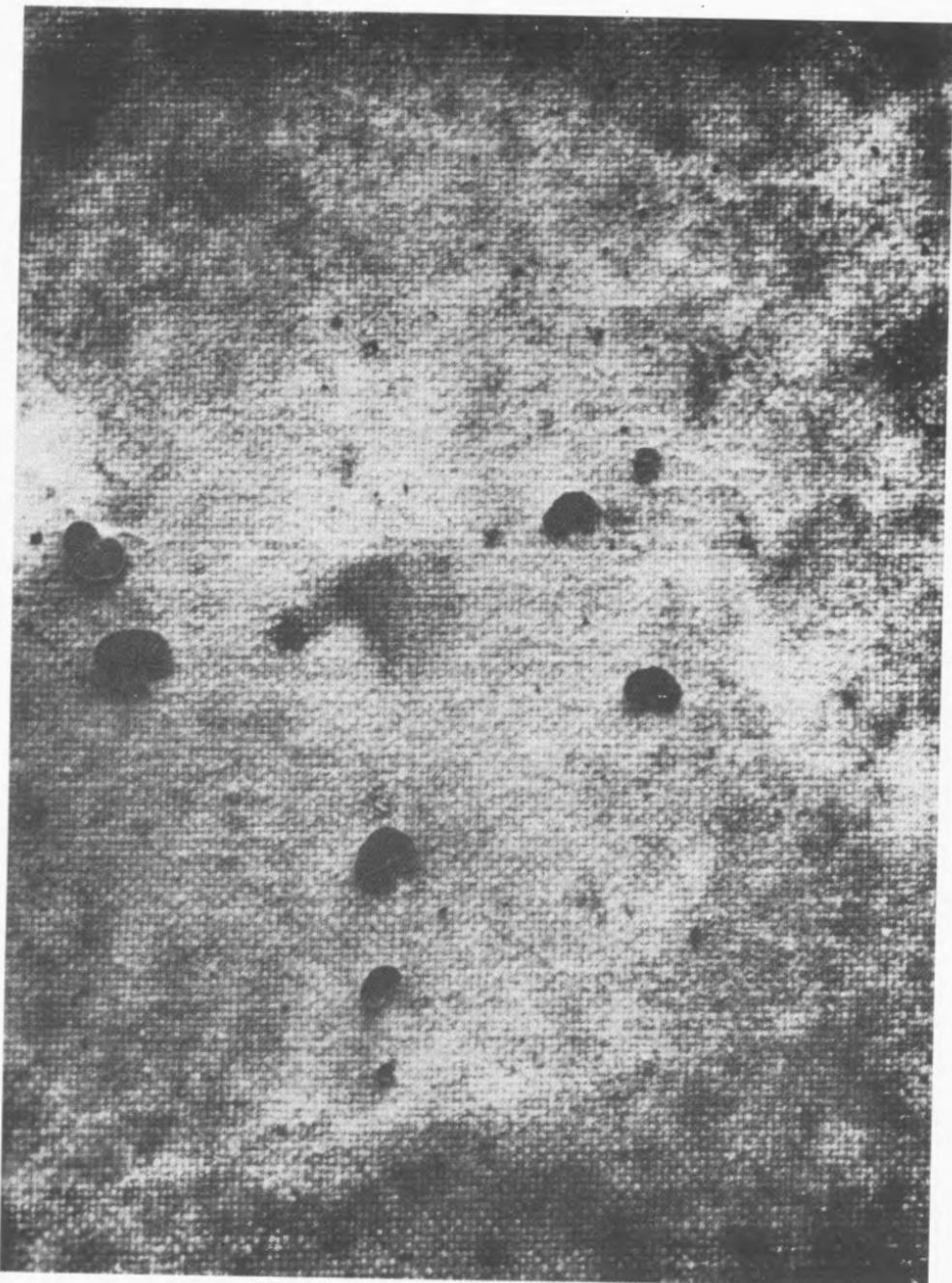
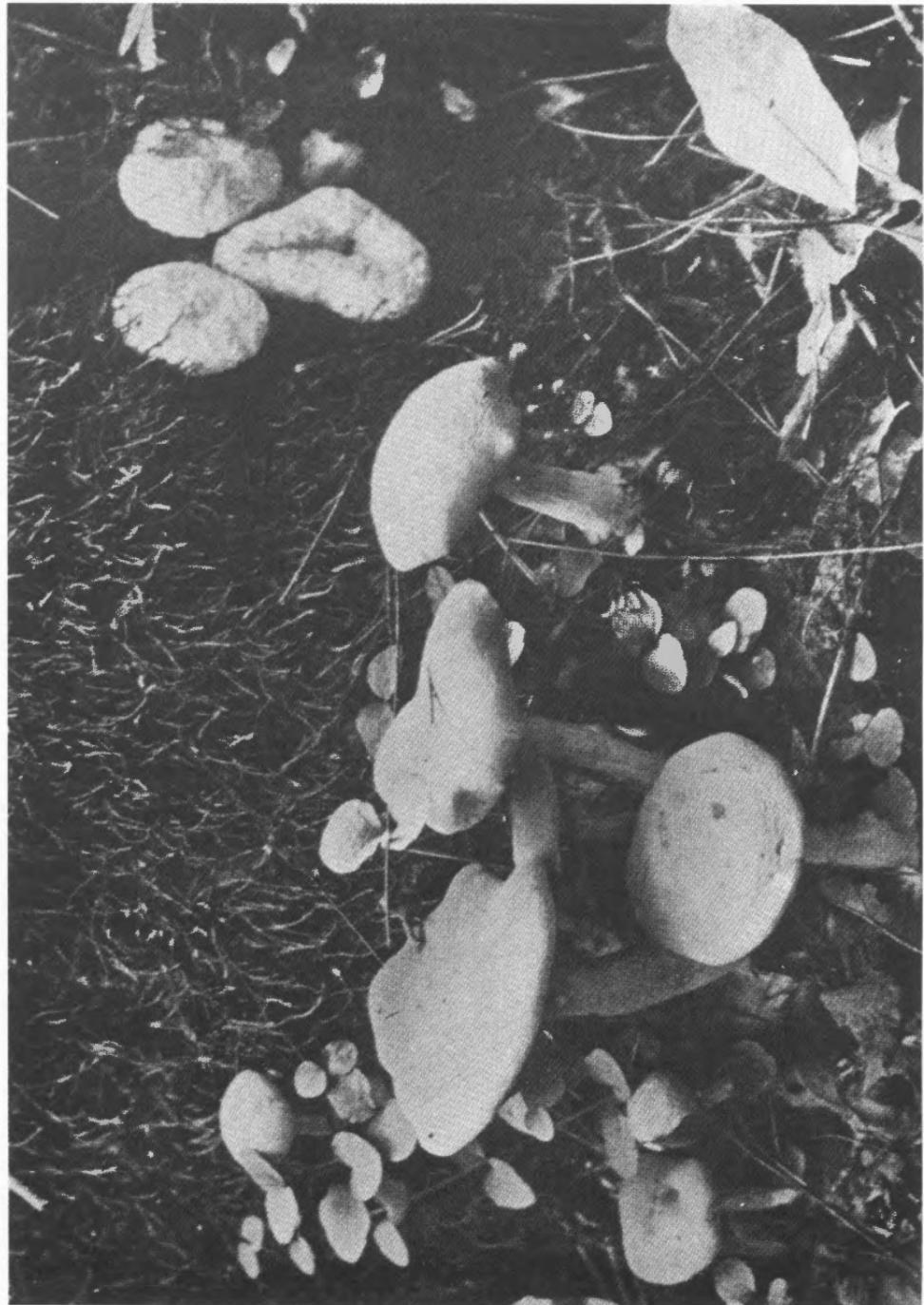


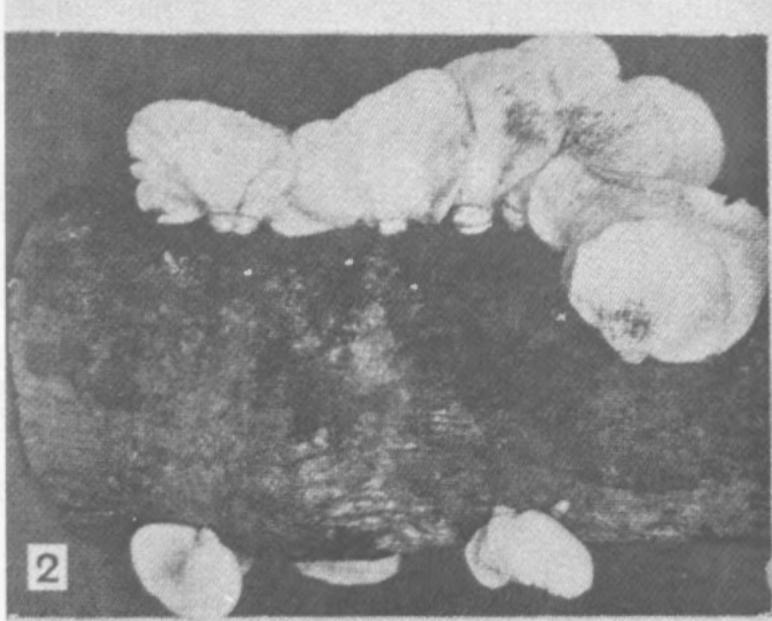
Plate 7



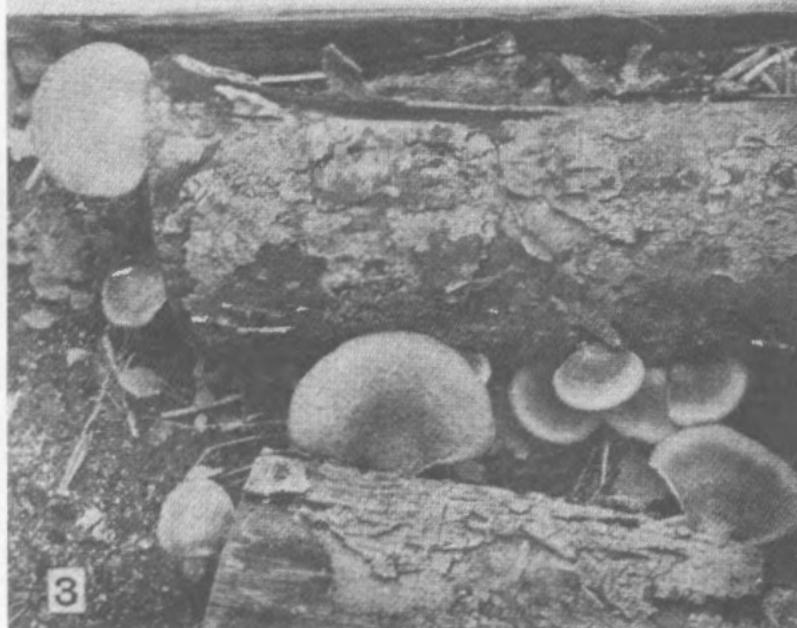
**Plate 8**



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Plate 9



Plate 10

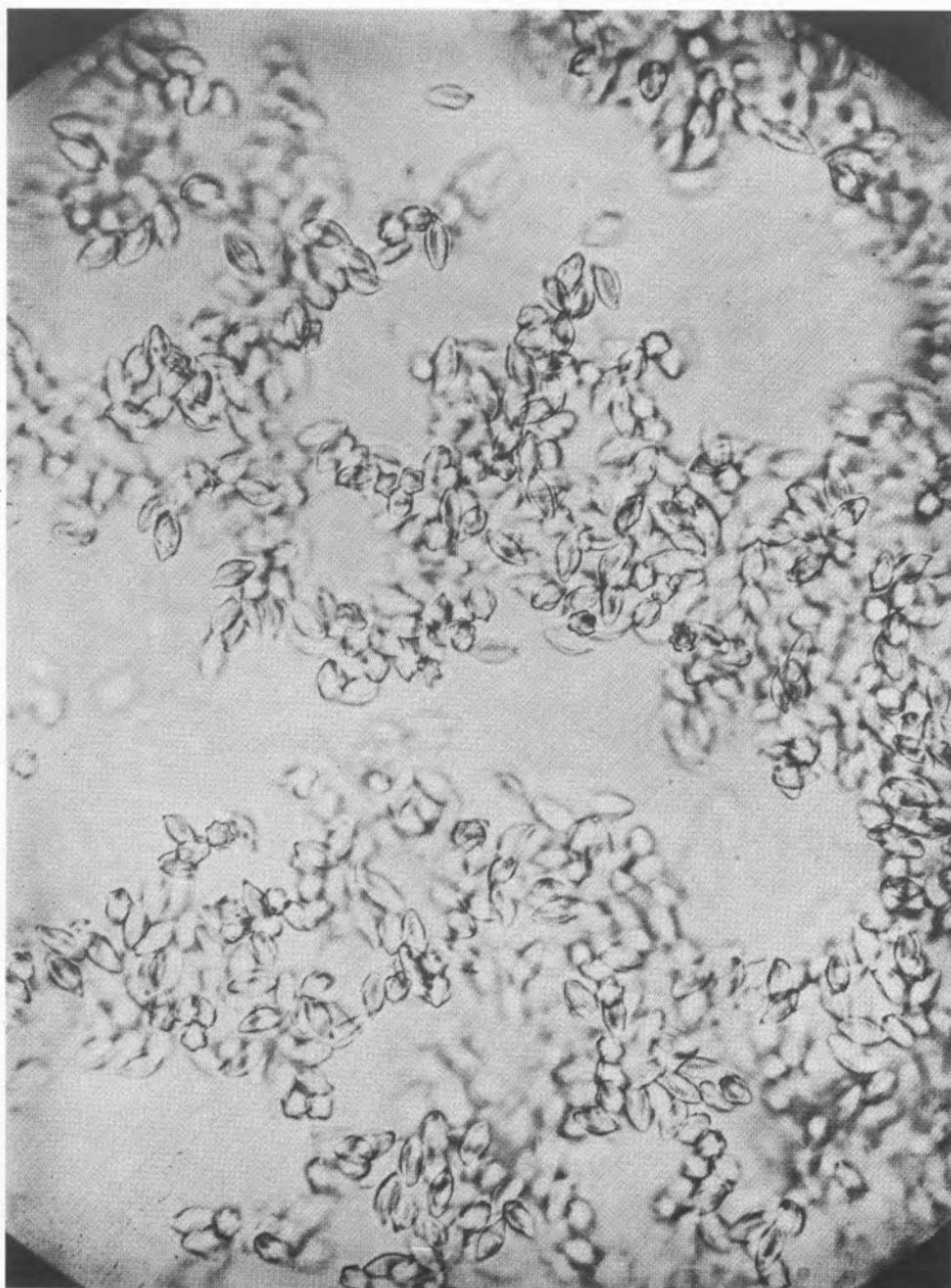


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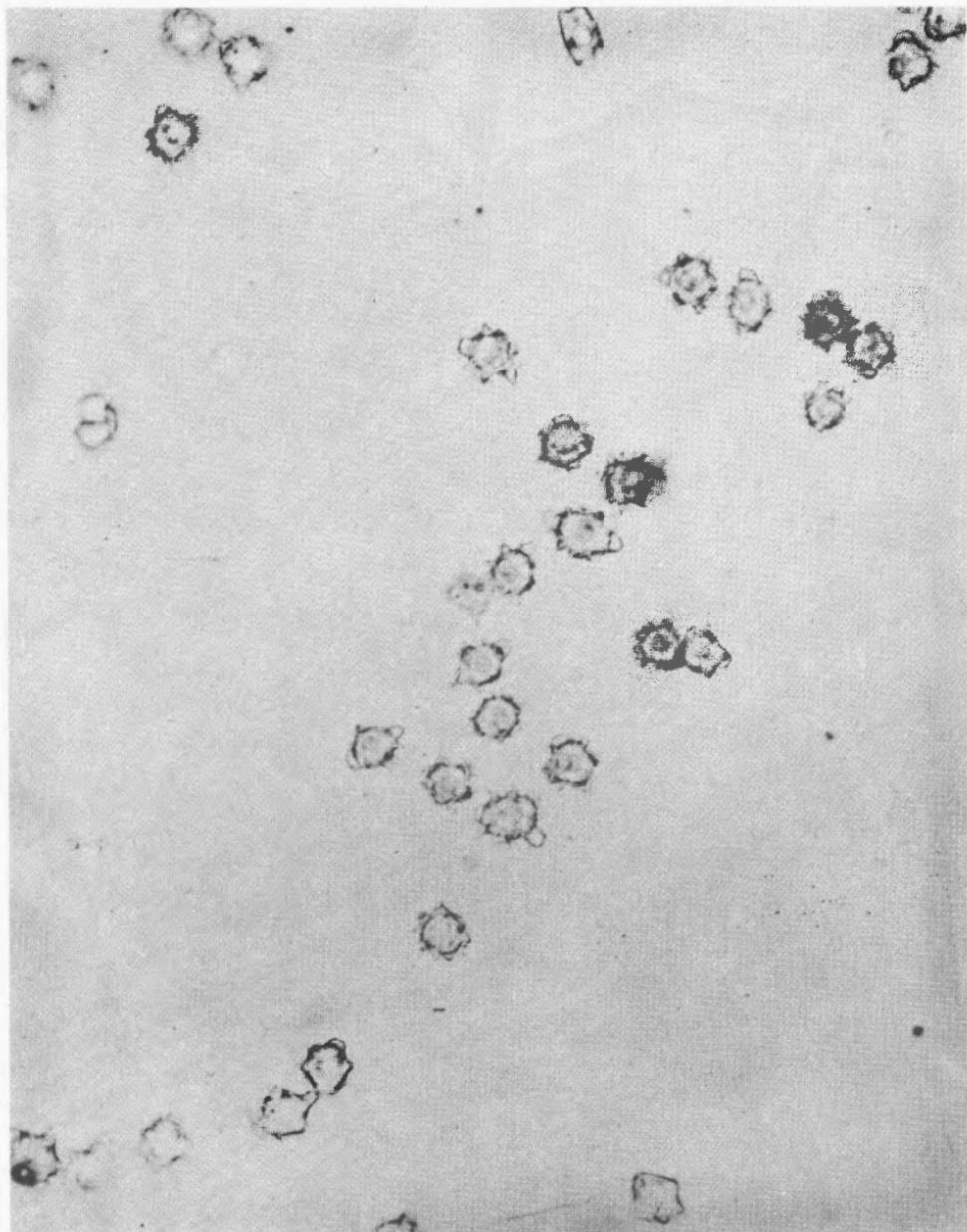
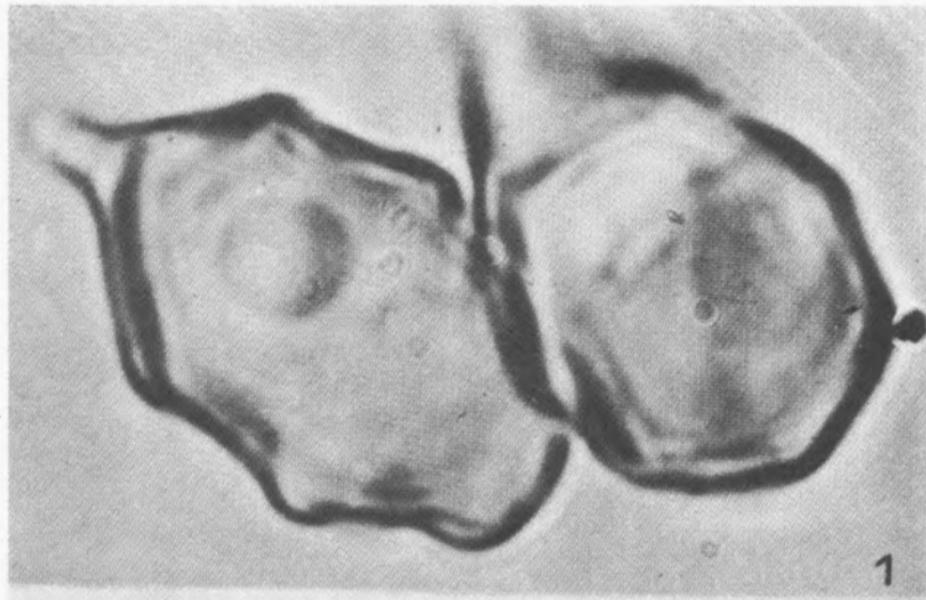
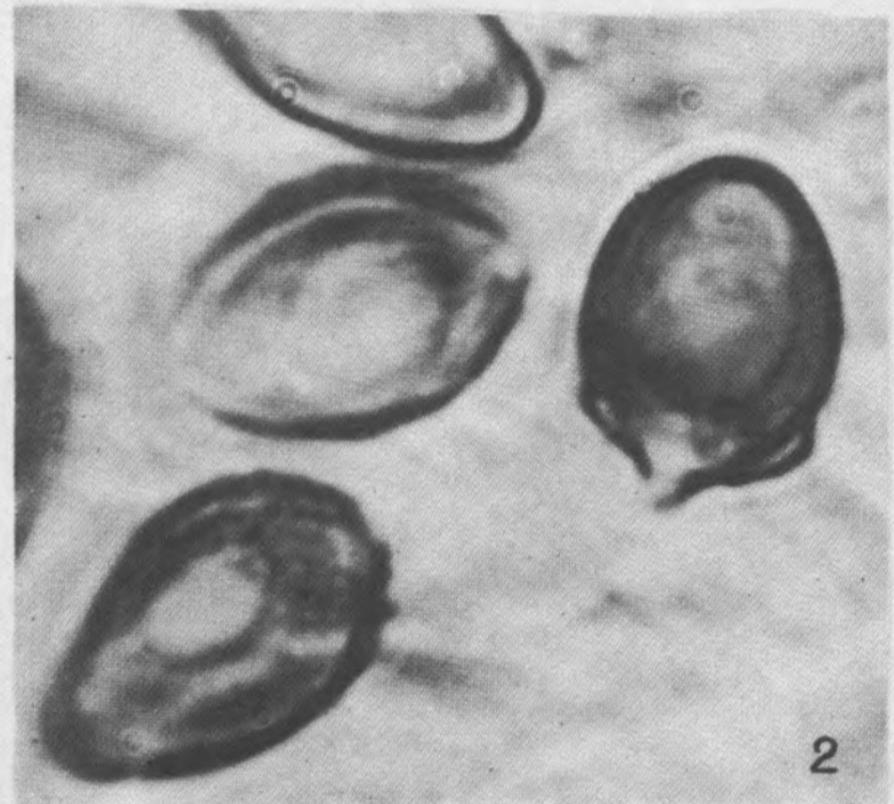


Plate 12



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Plate 13

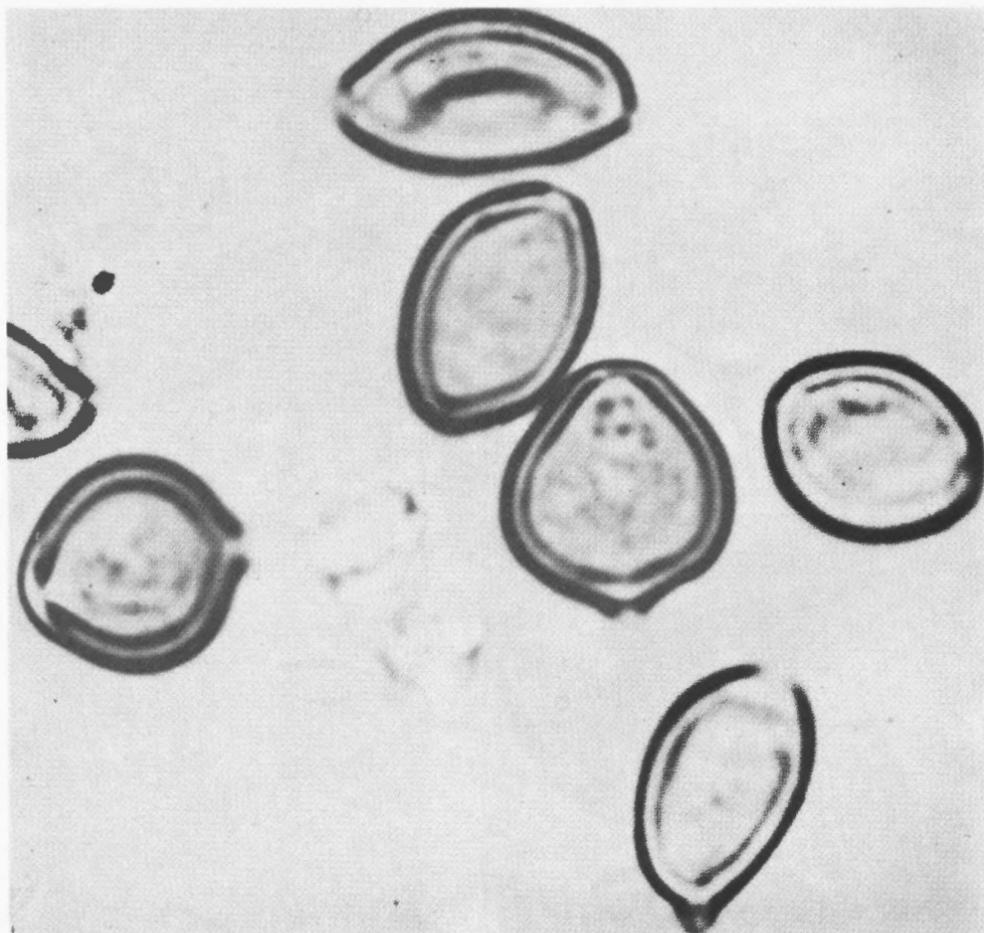


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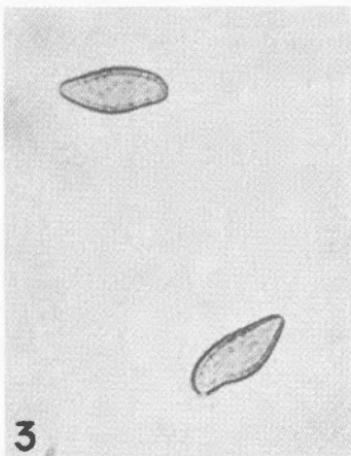
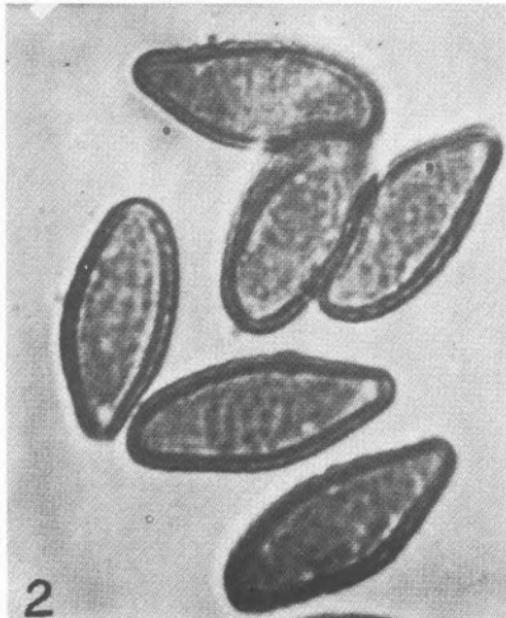
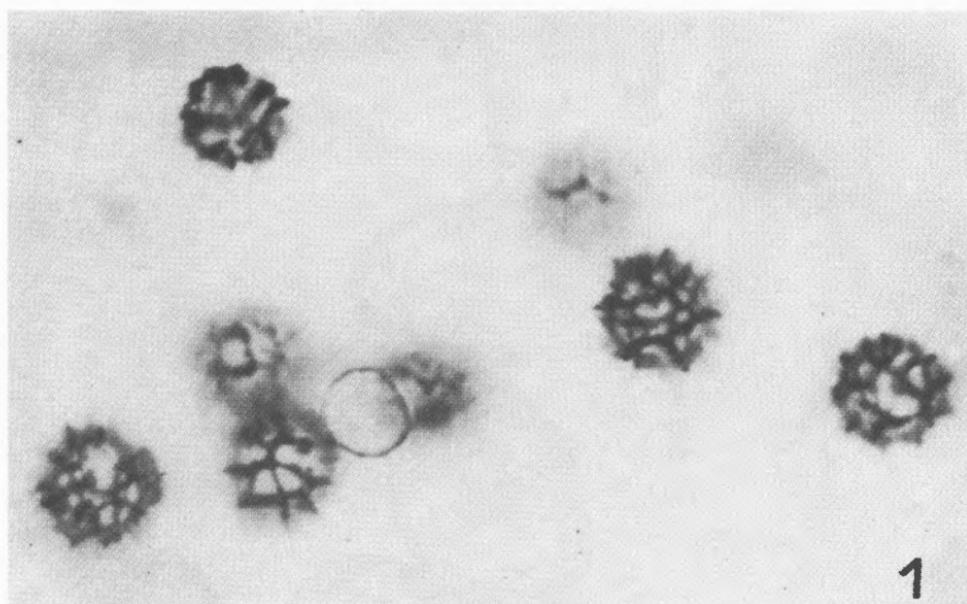


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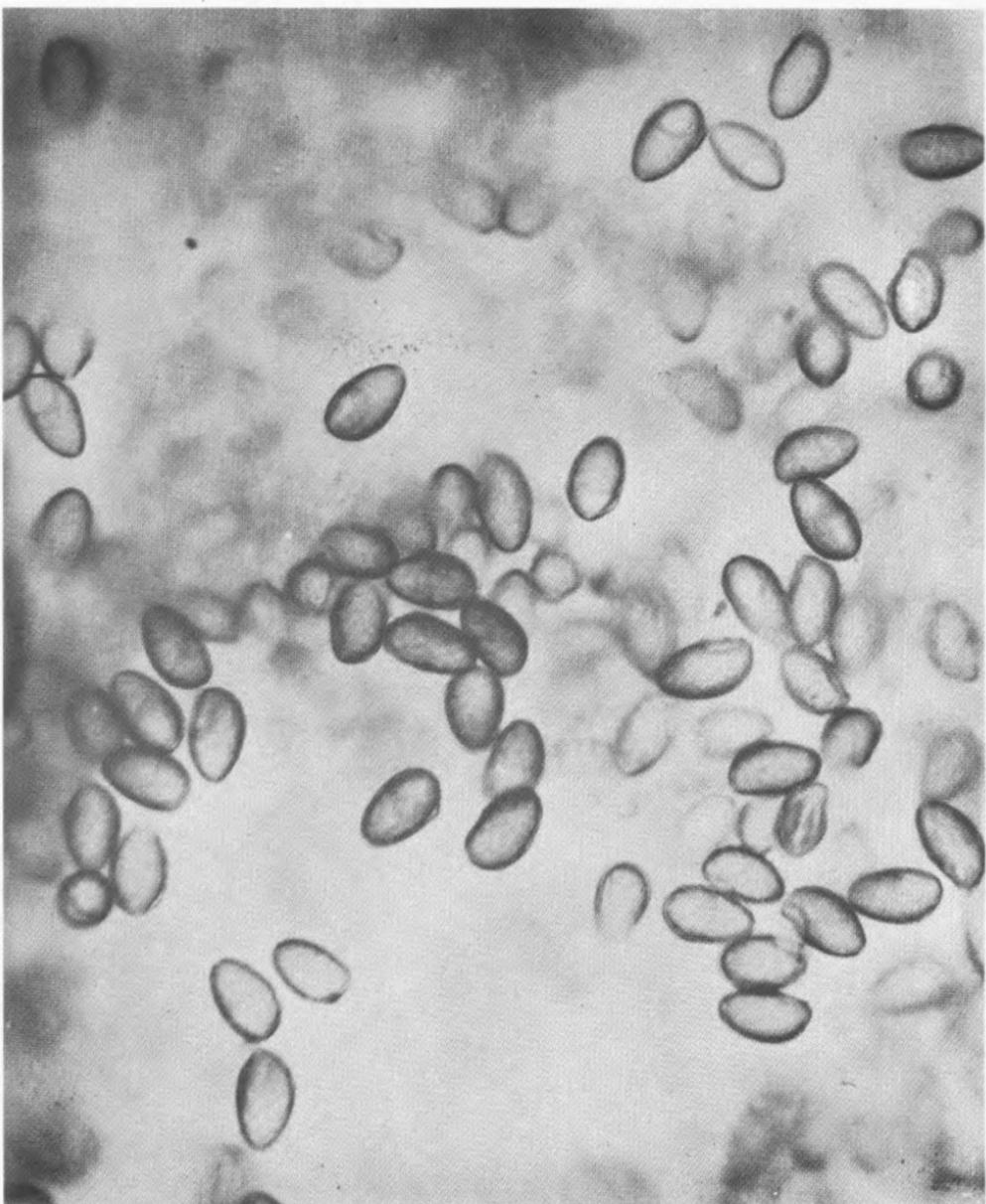


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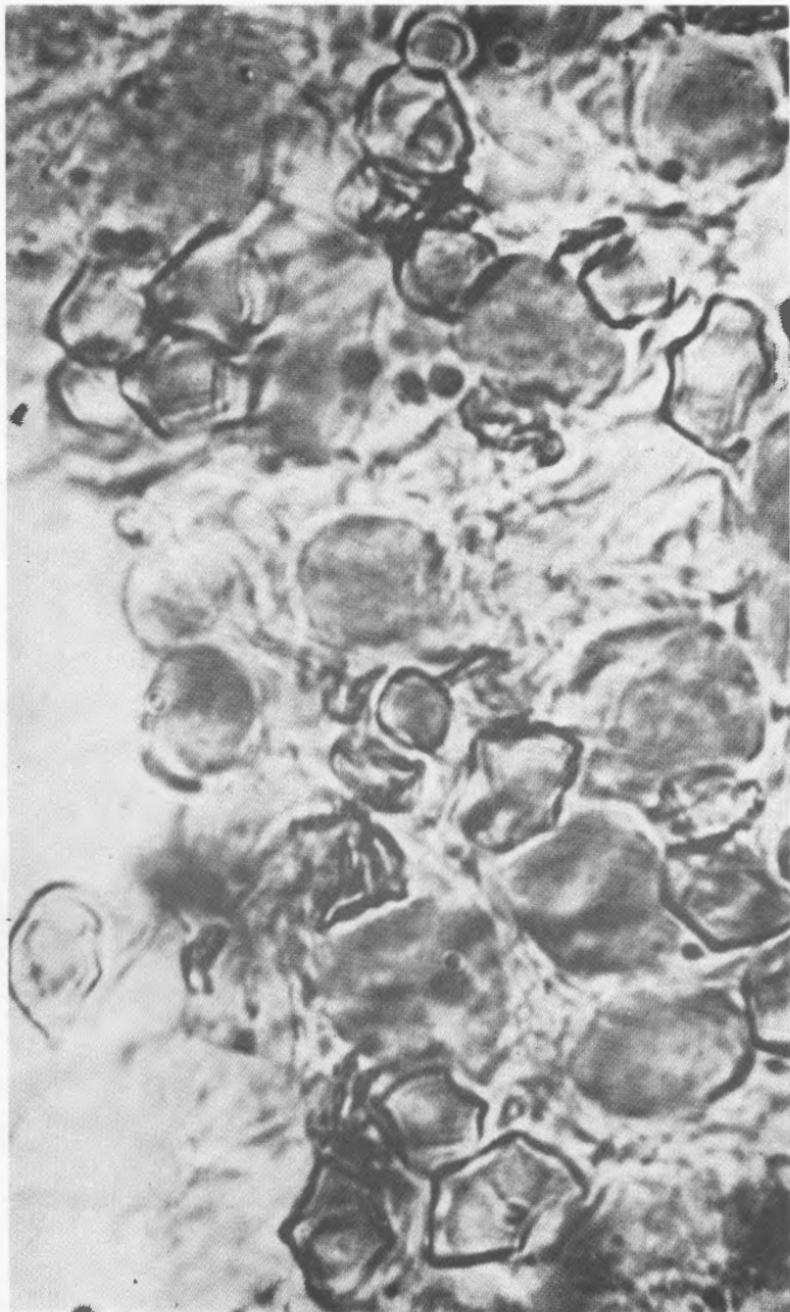




Plate 18

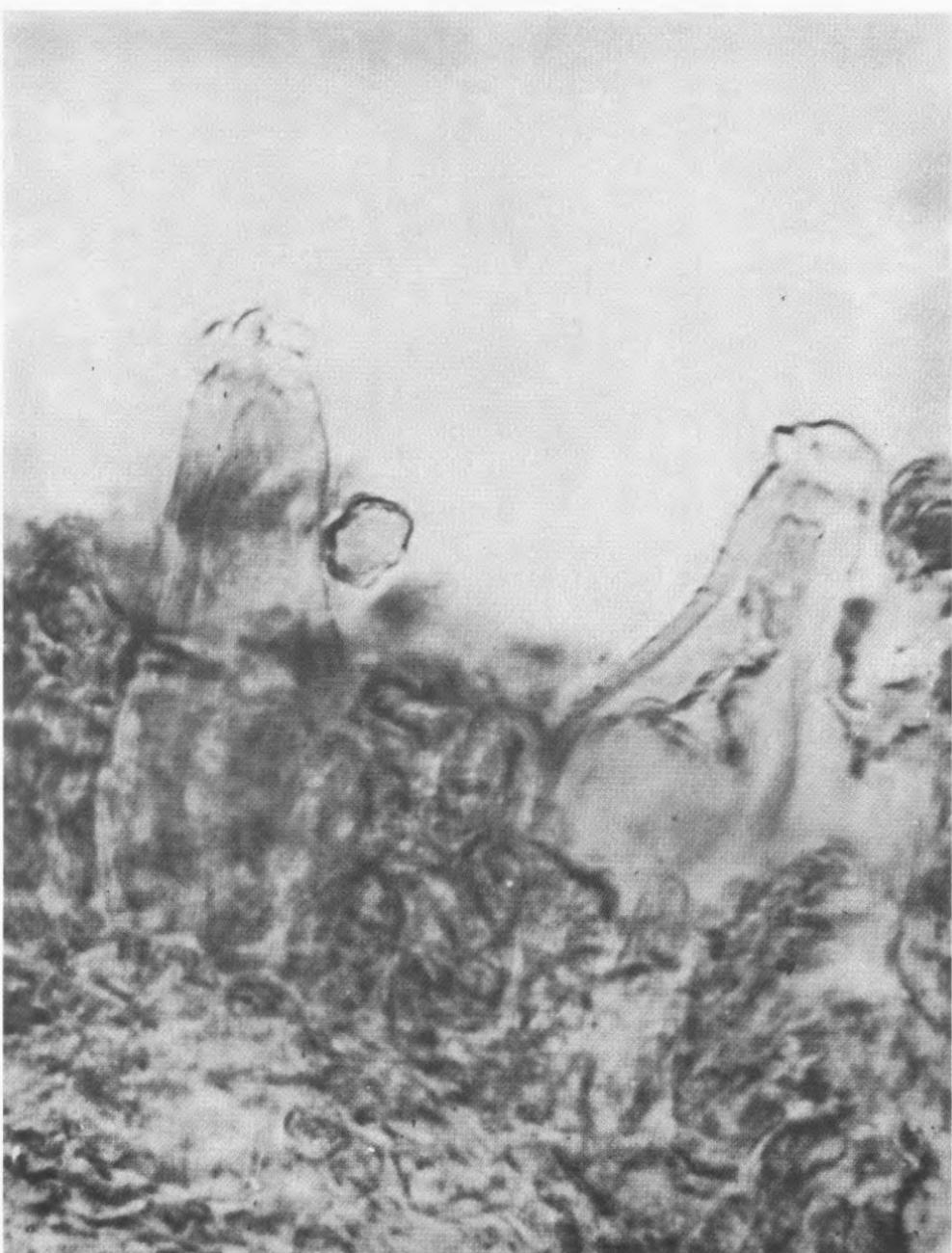


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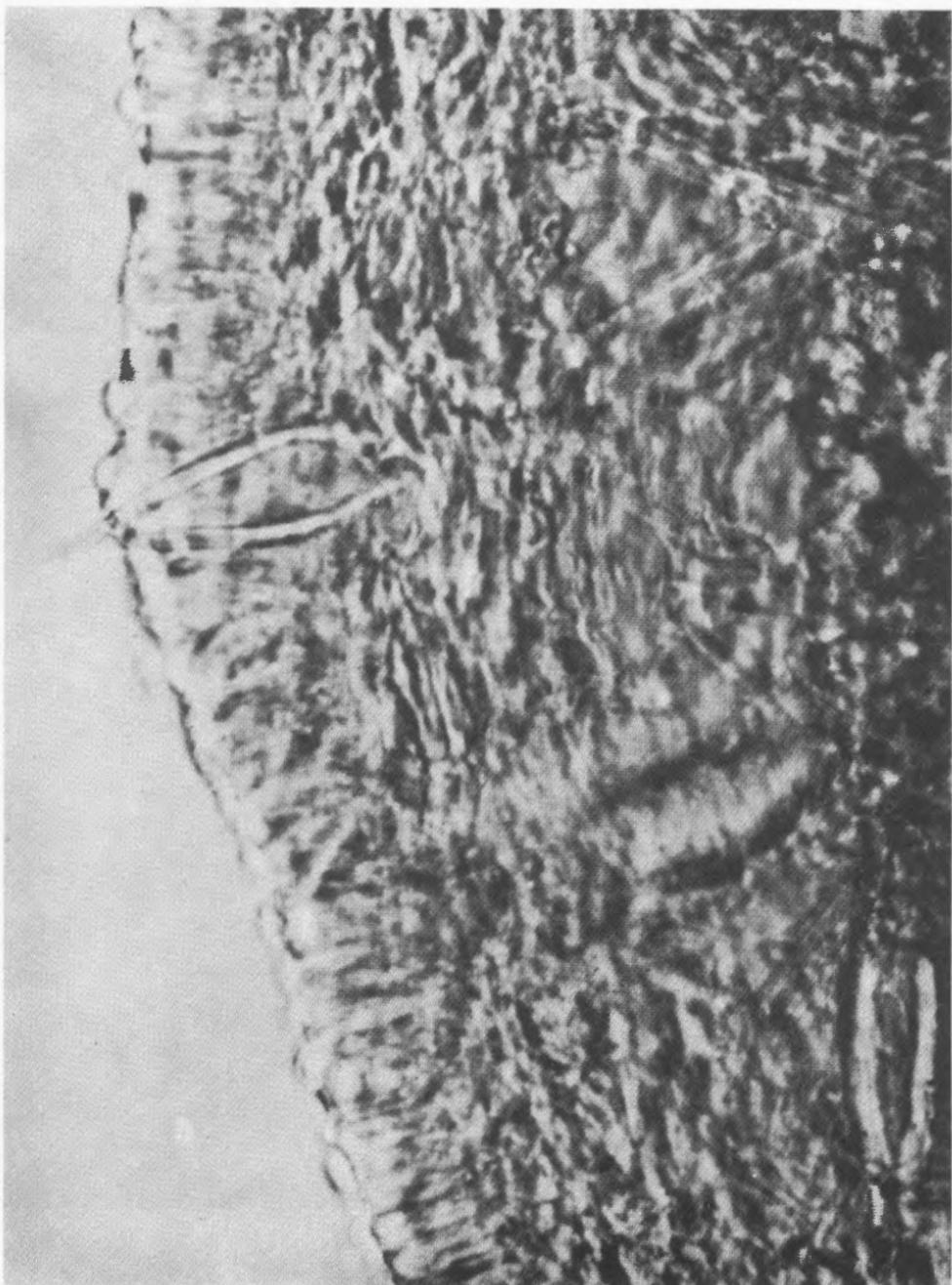


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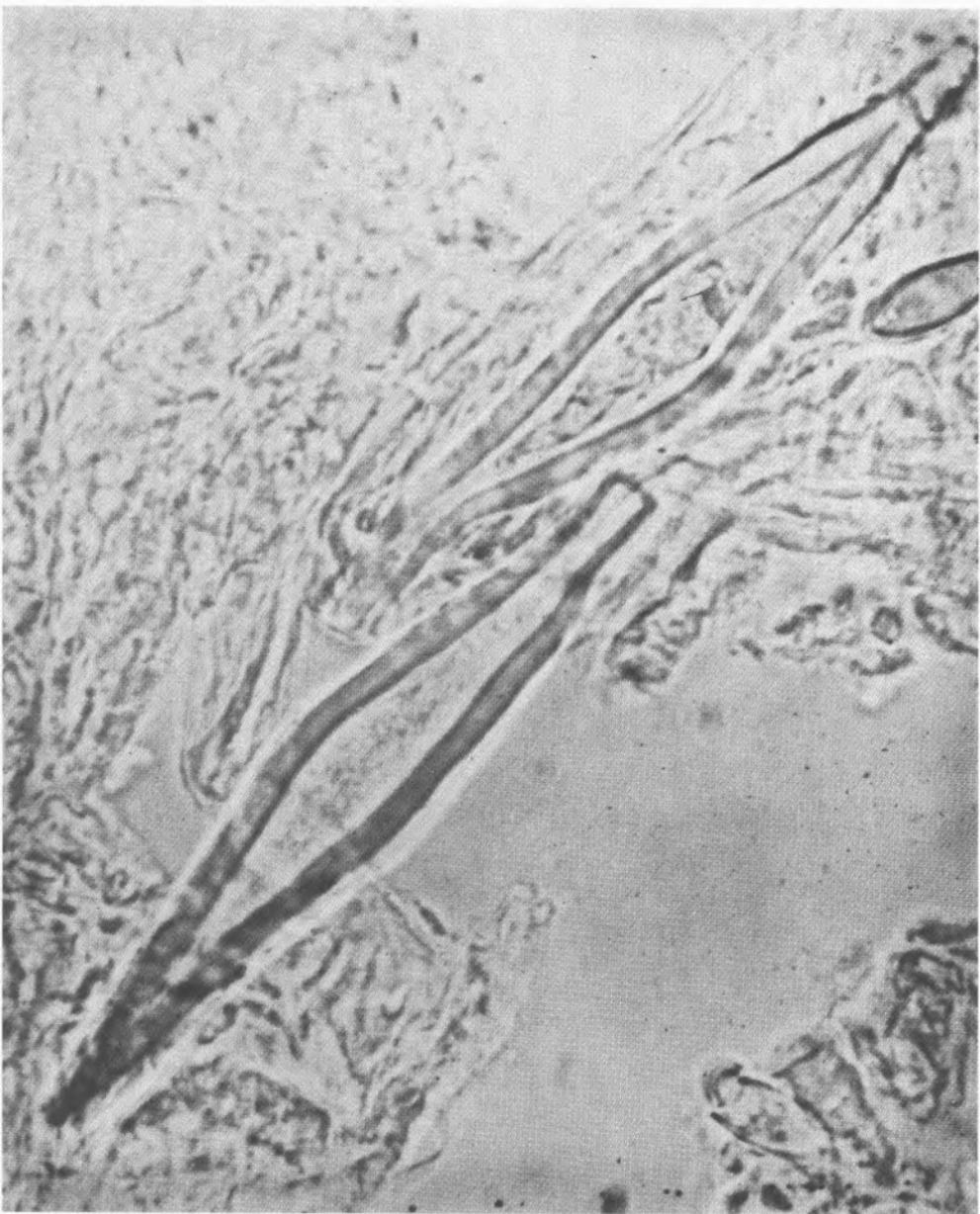
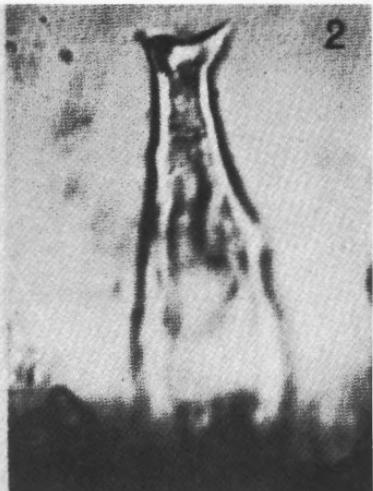
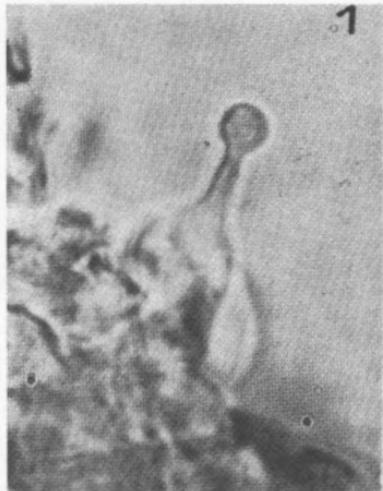


Plate 21



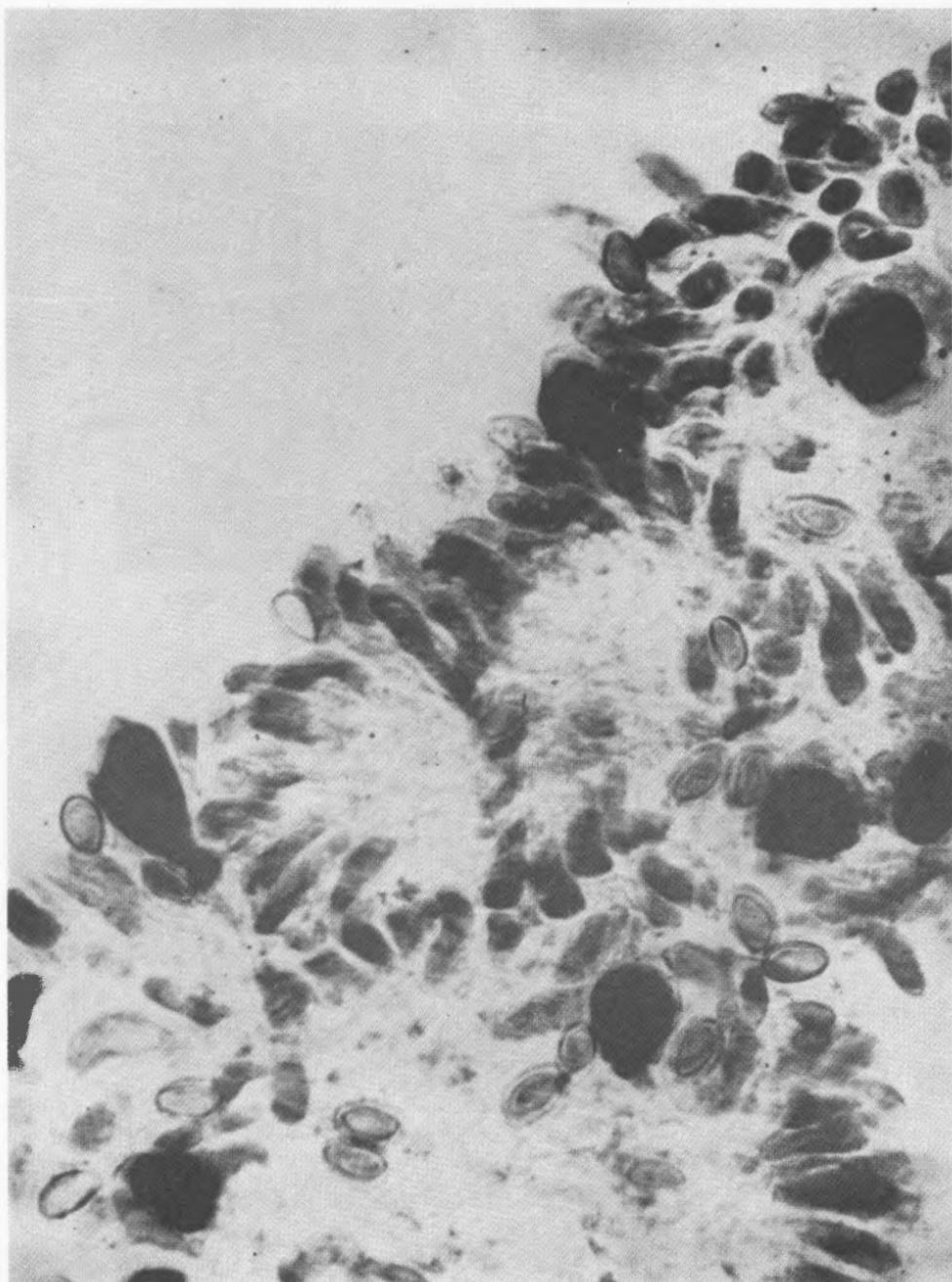


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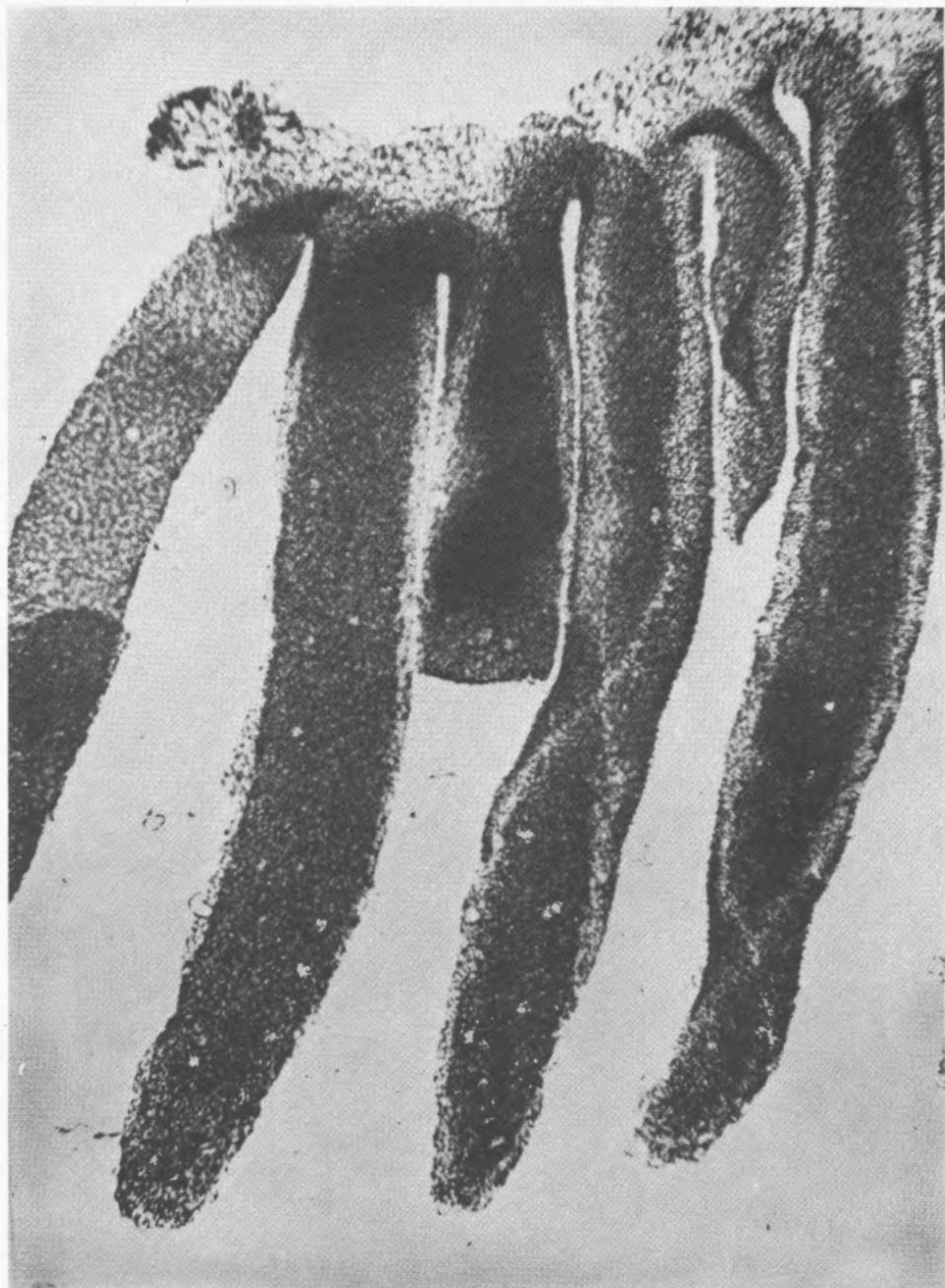


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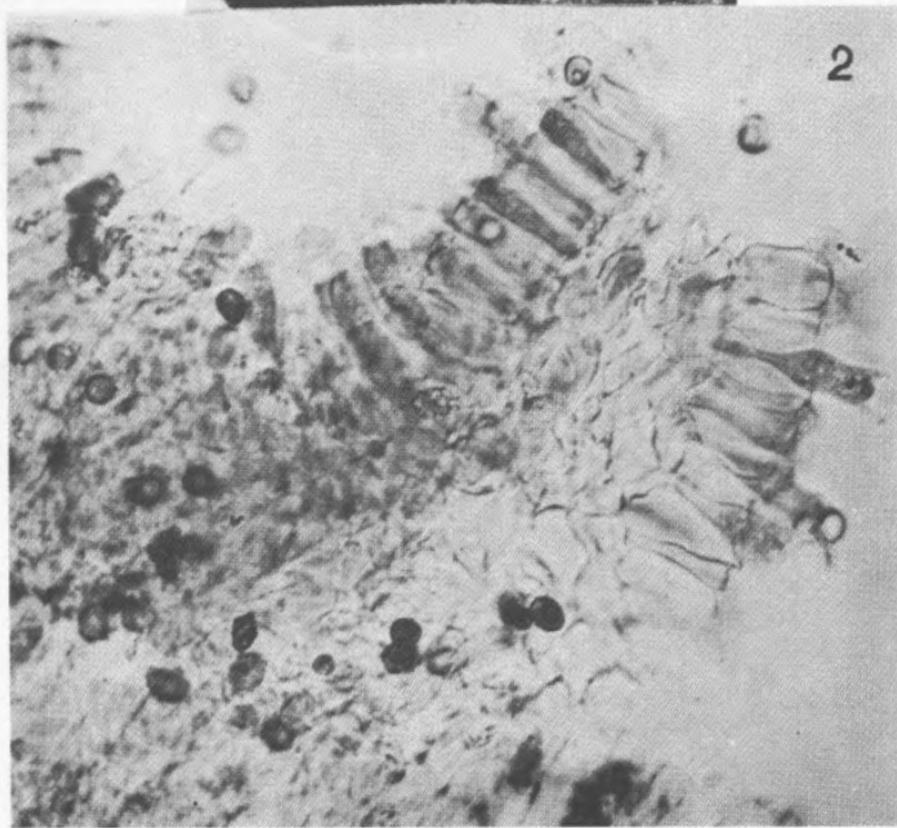
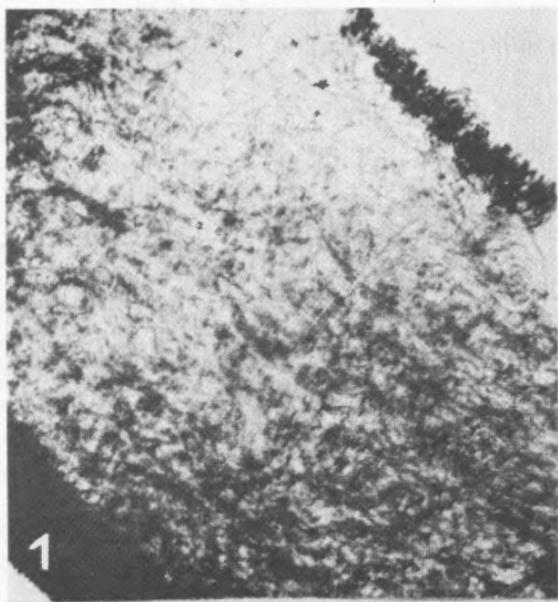


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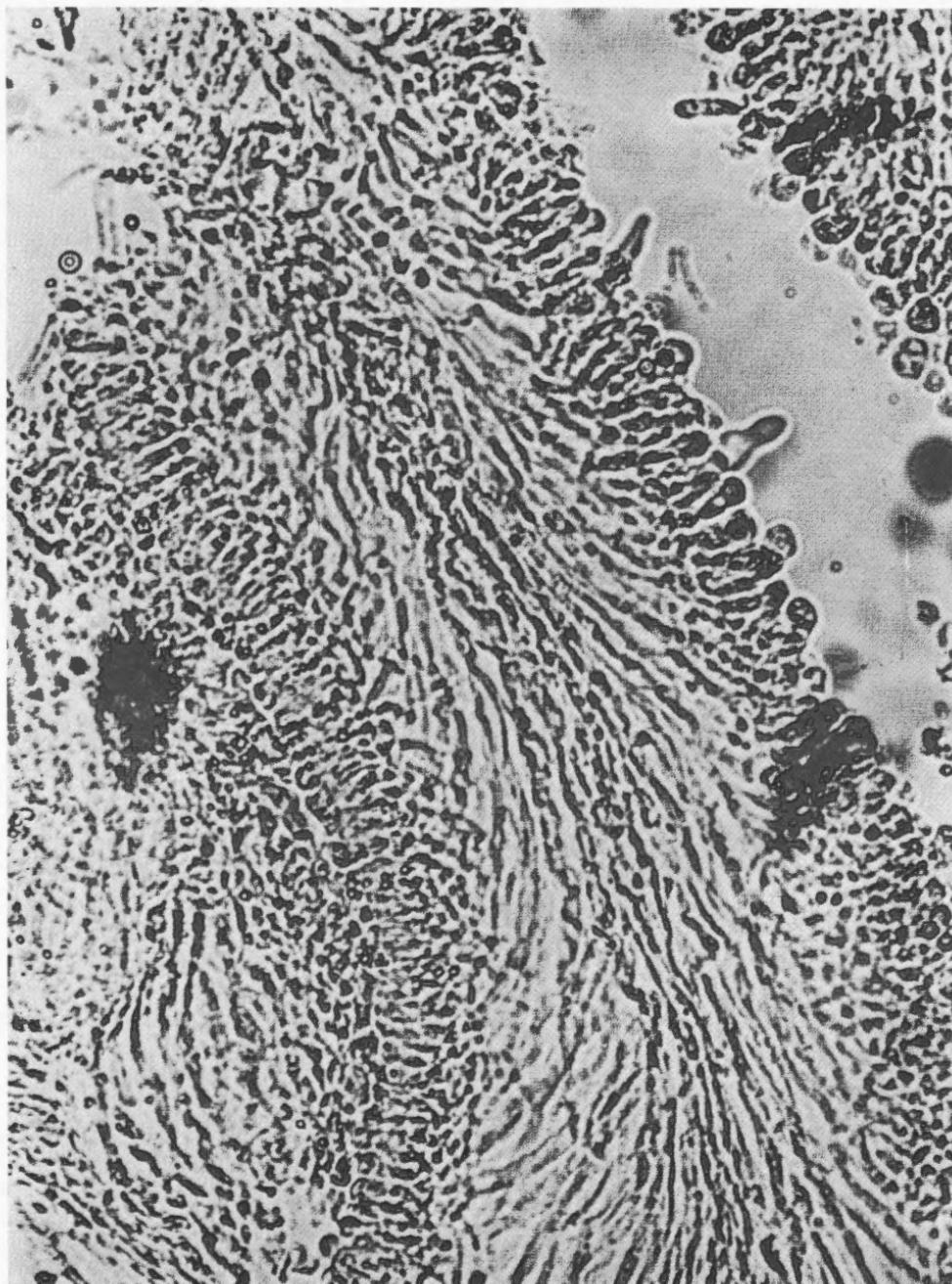


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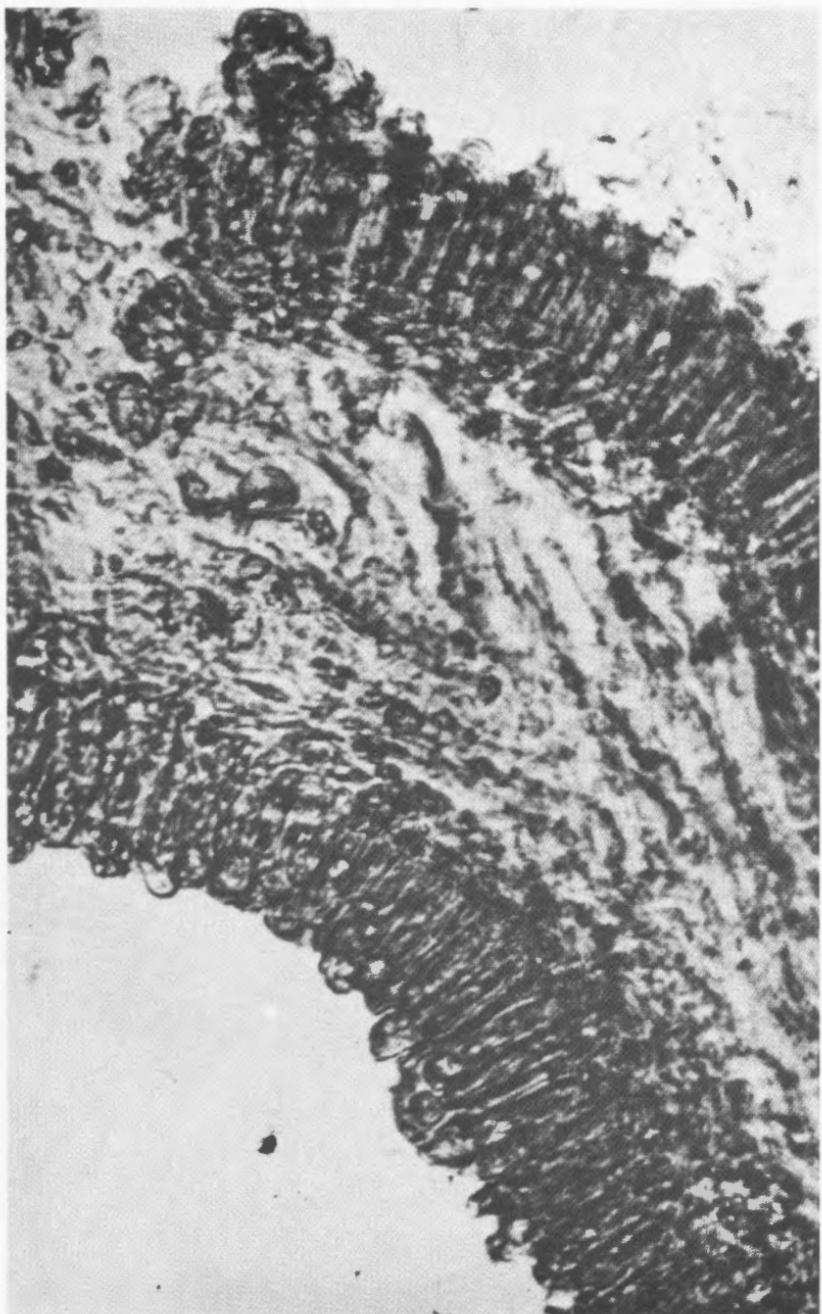


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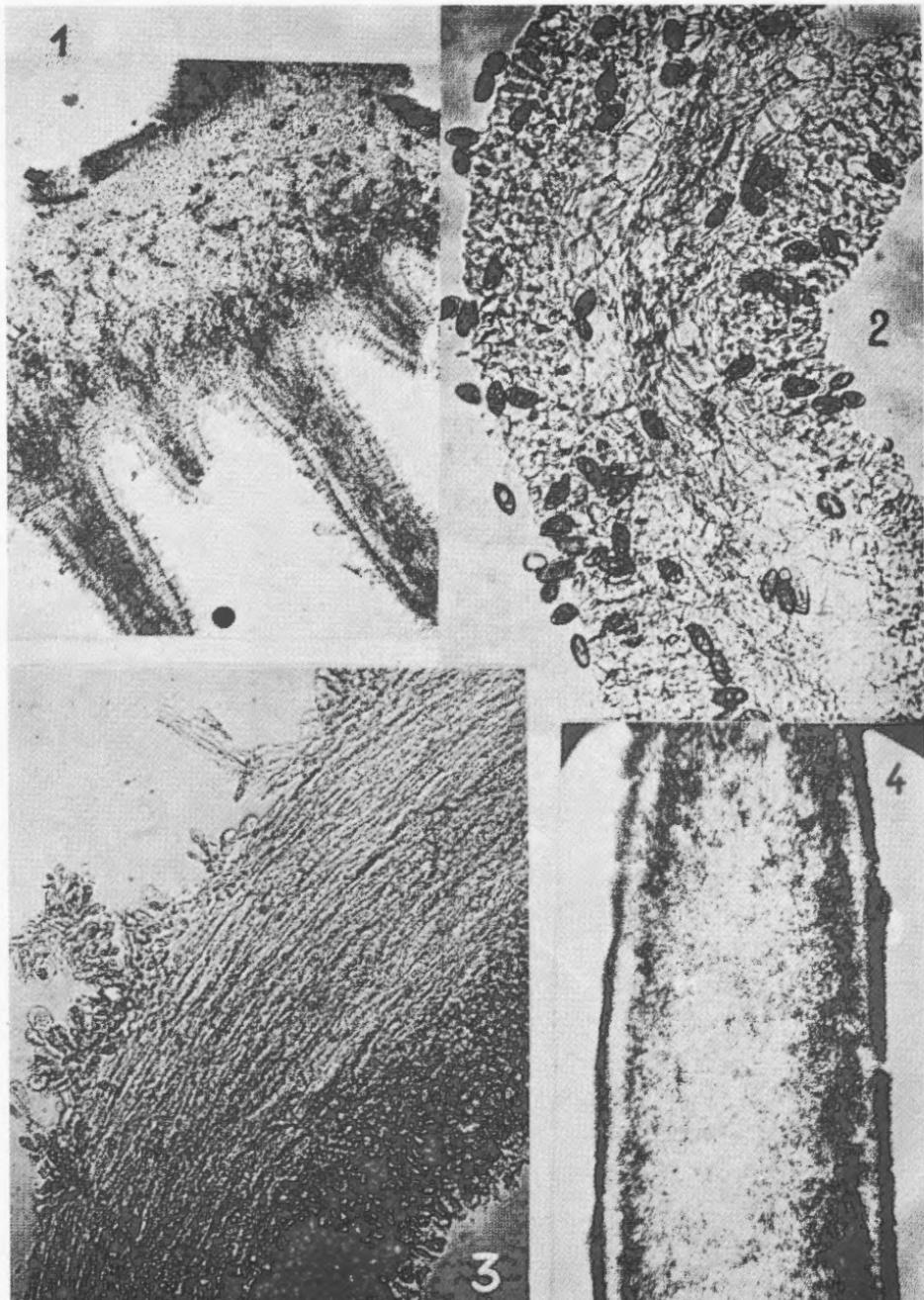


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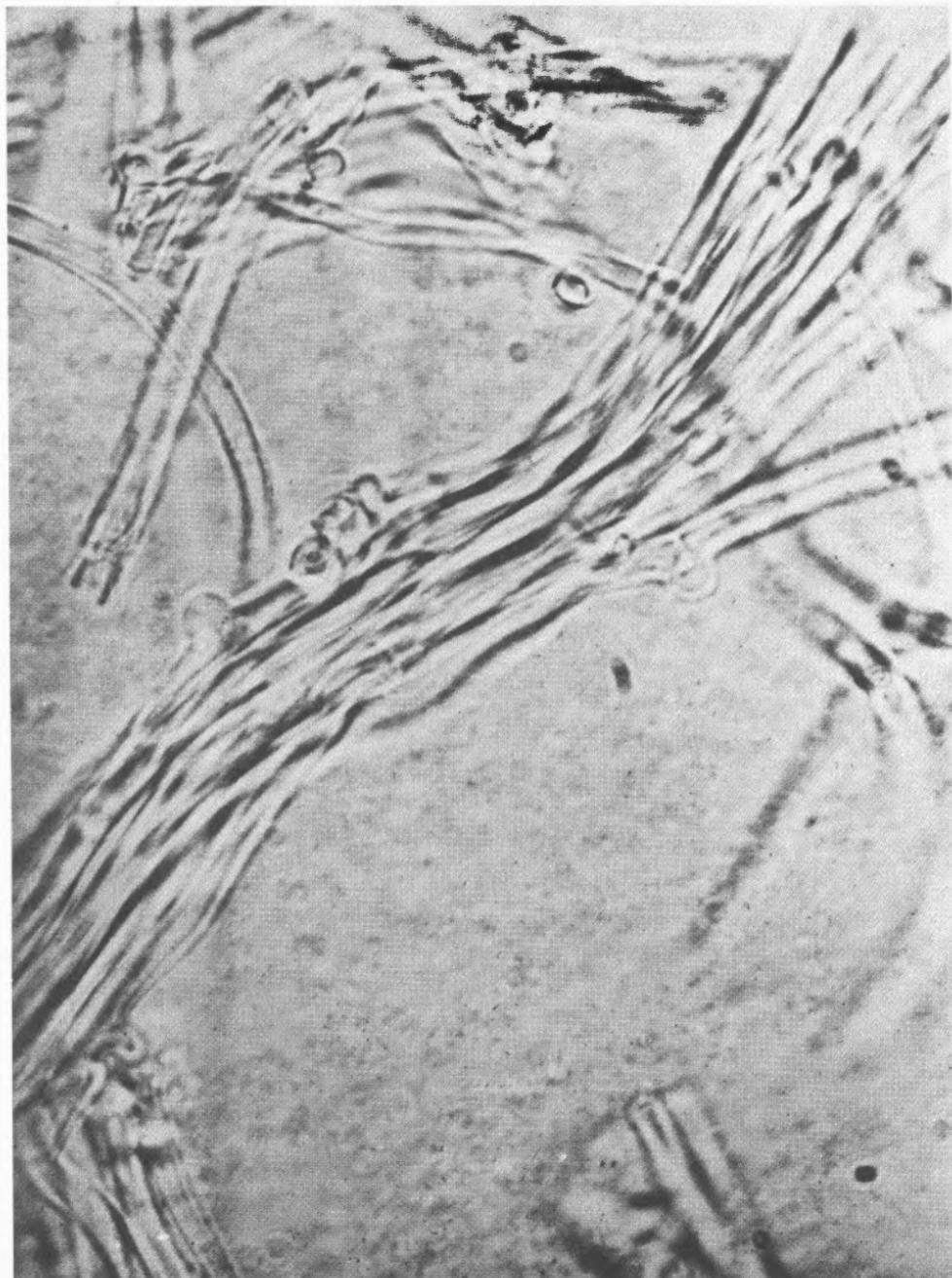


Plate 29



Plate 30

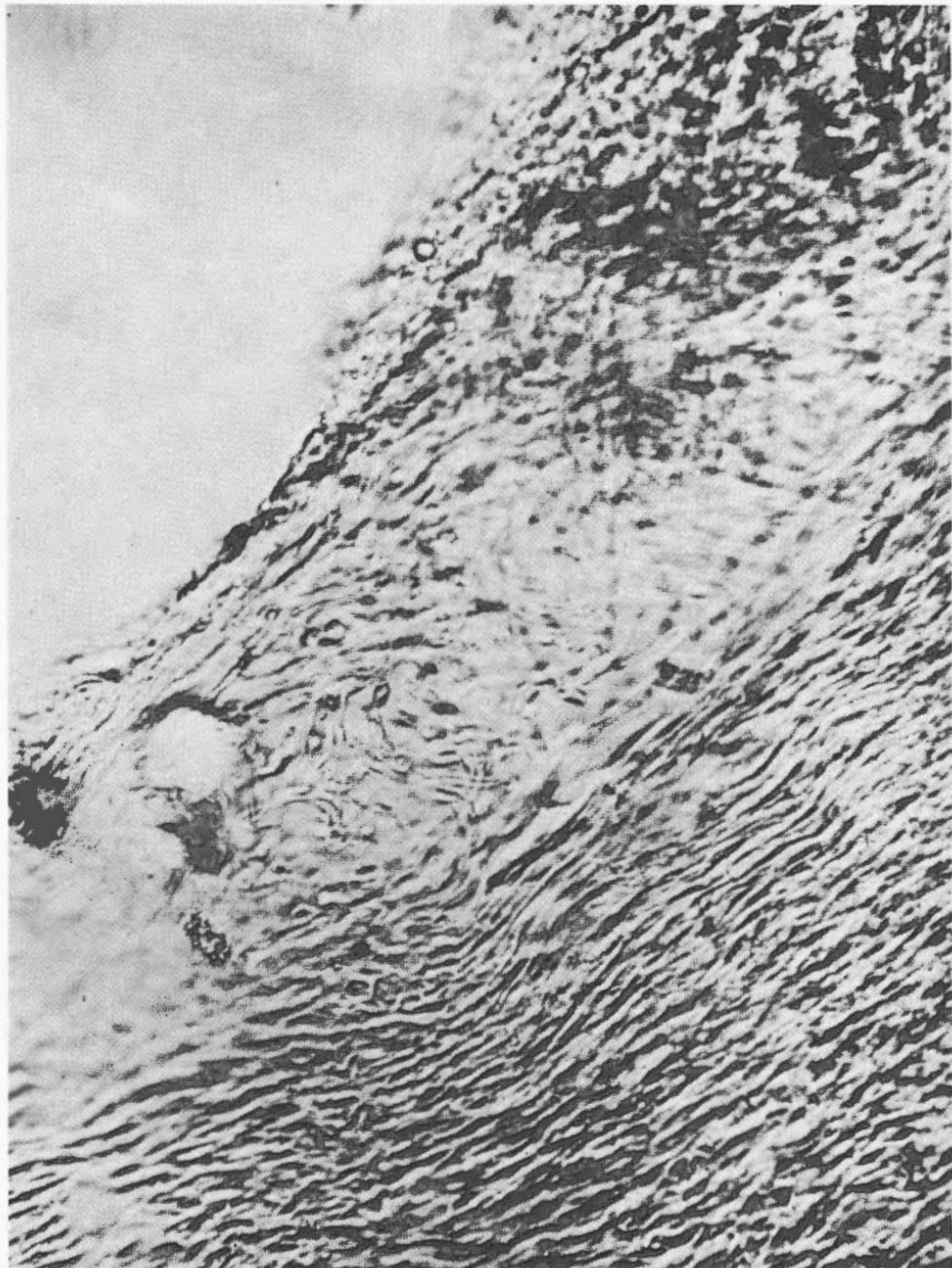


Plate 31



Plate 32

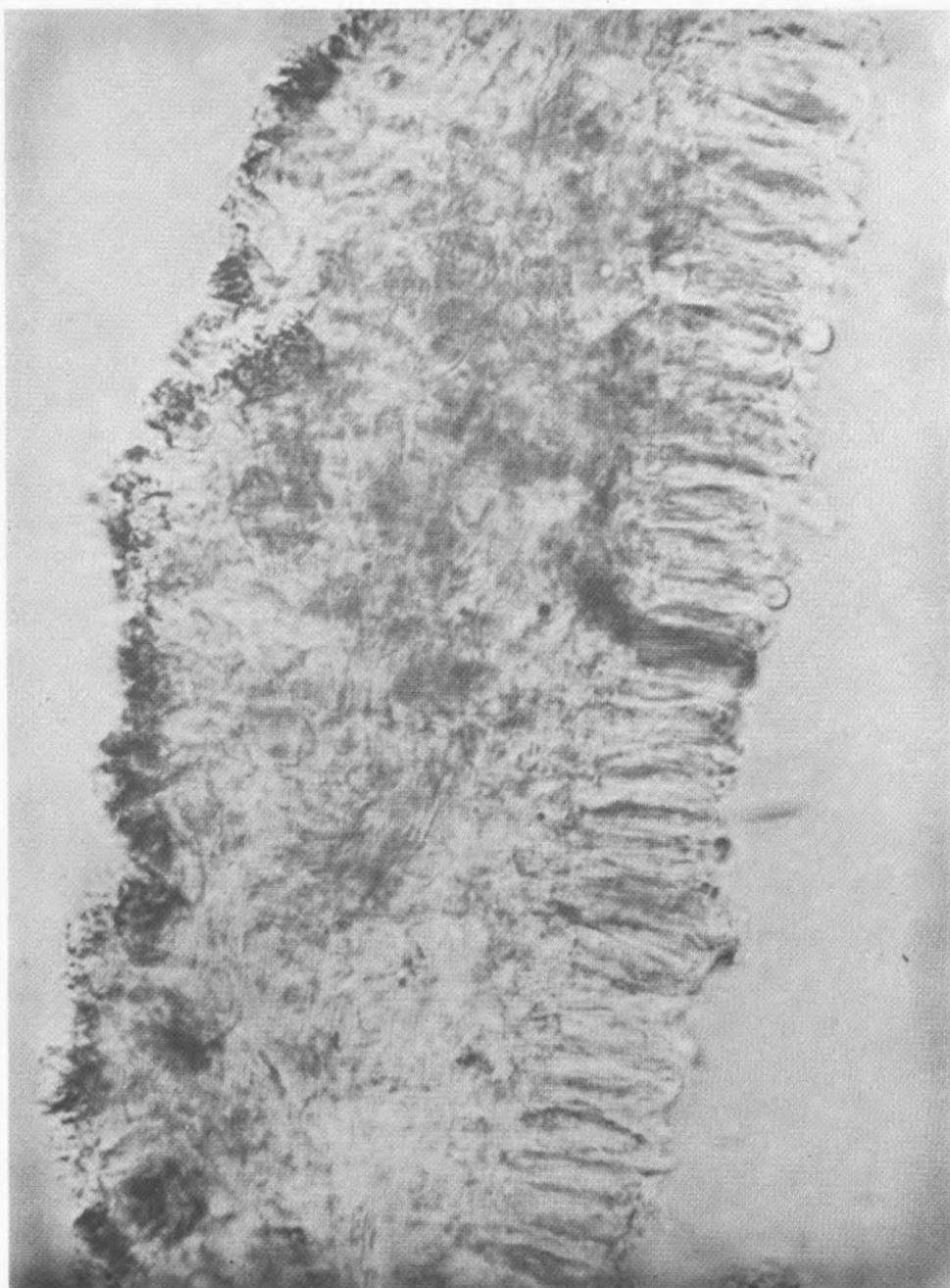
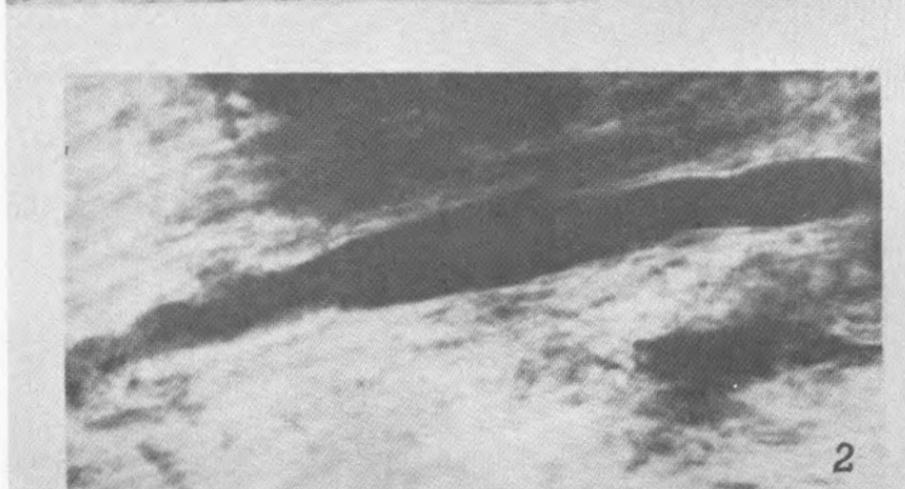


Plate 33



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Plate 34

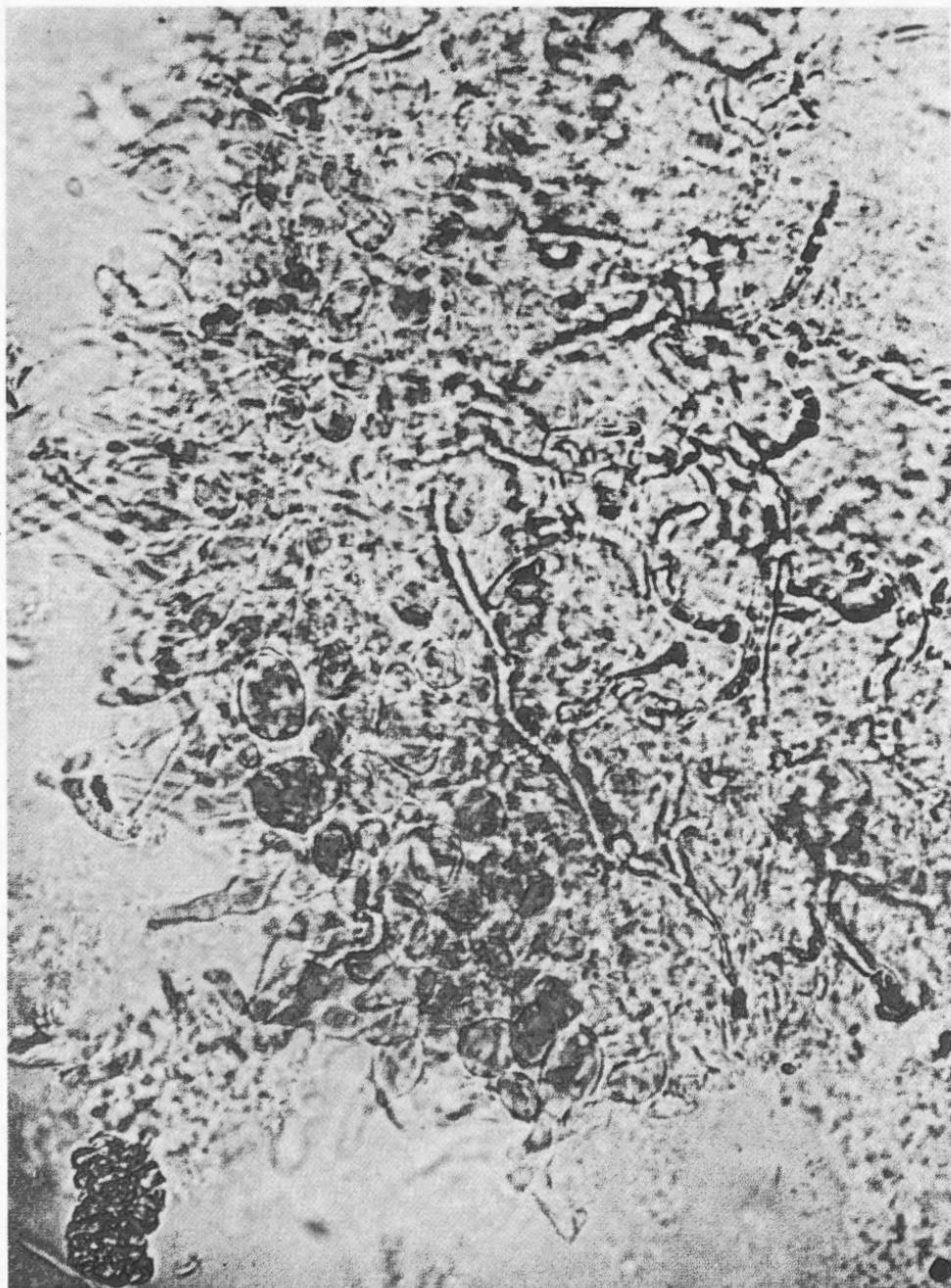


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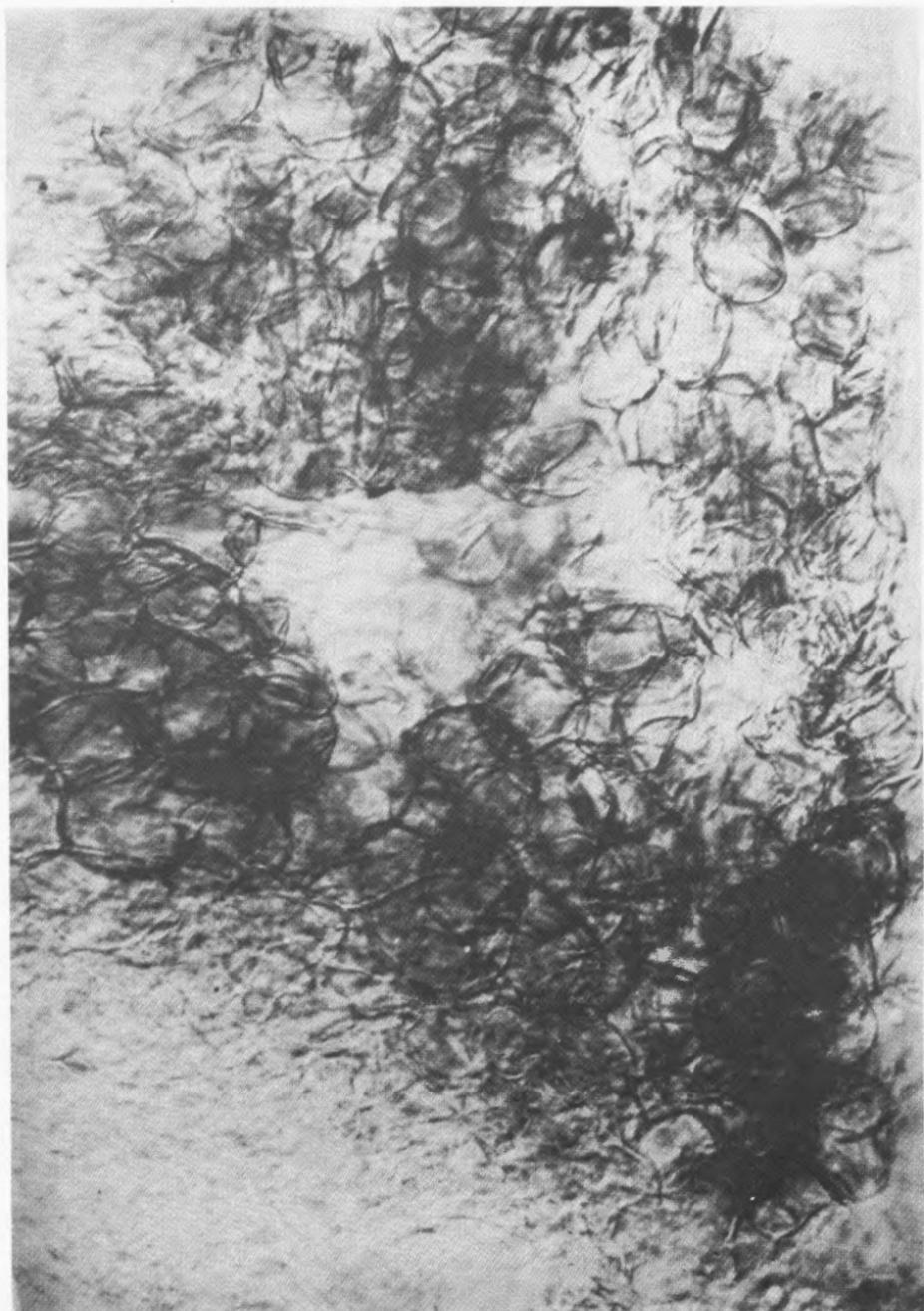


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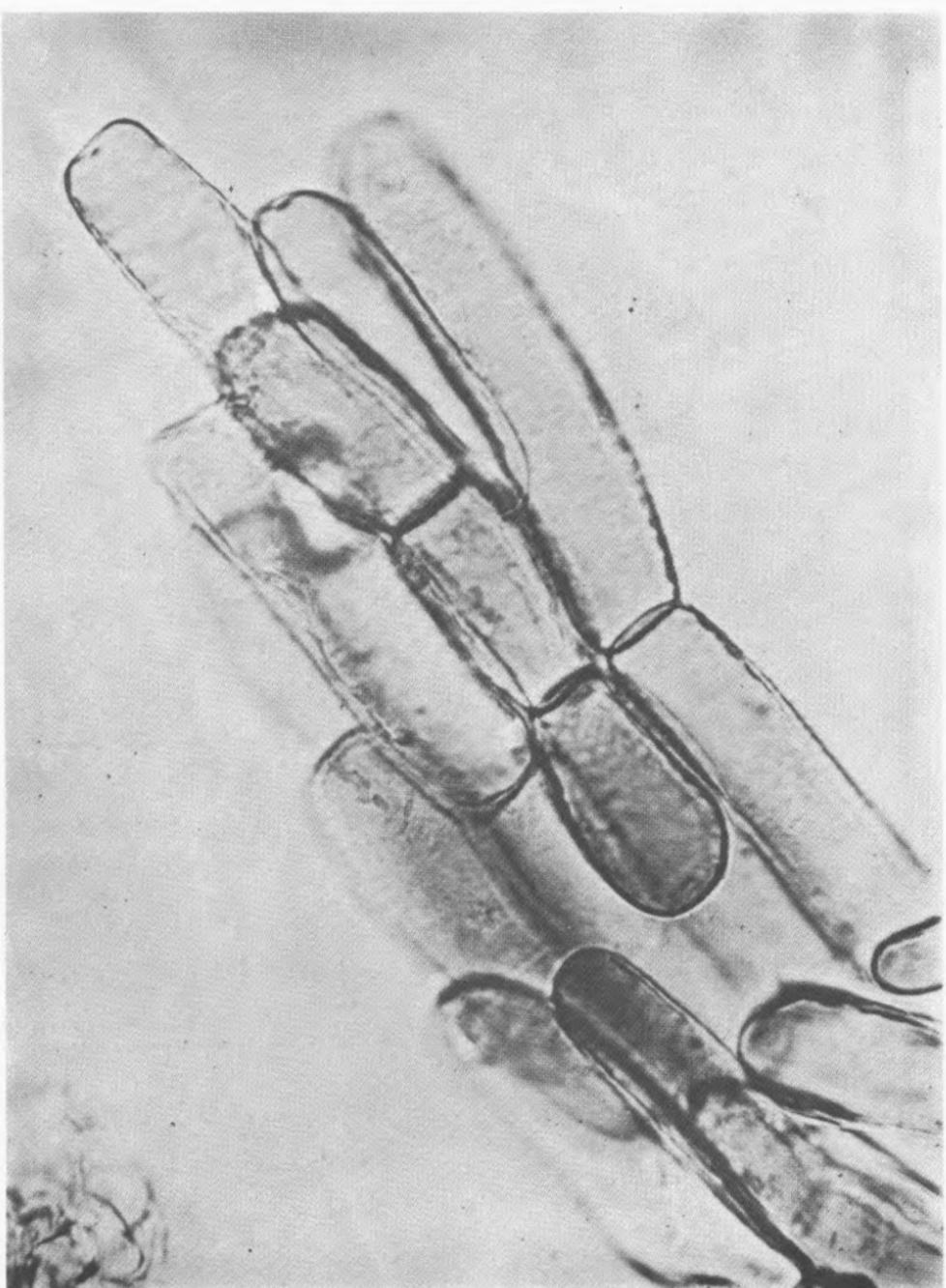


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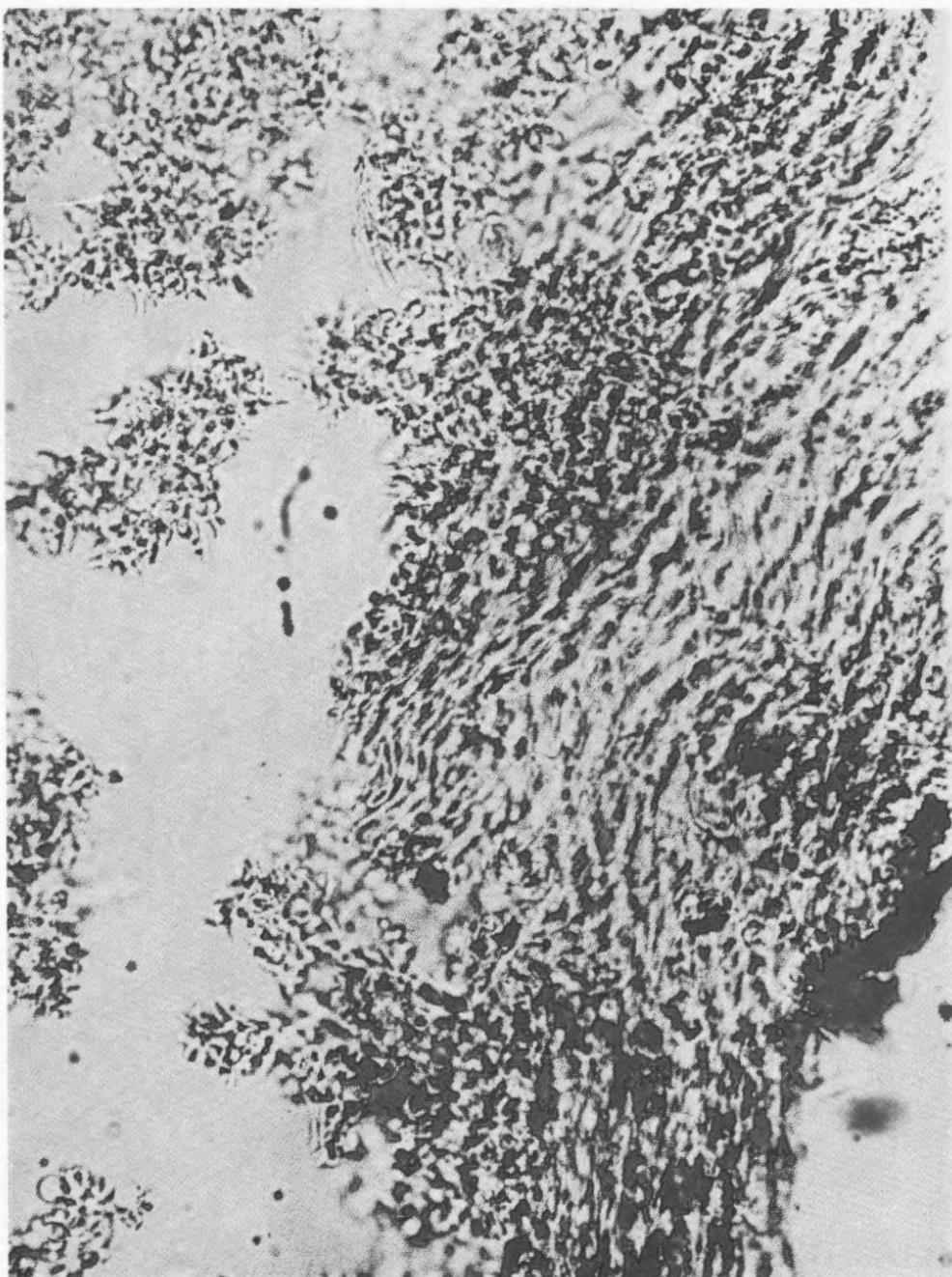


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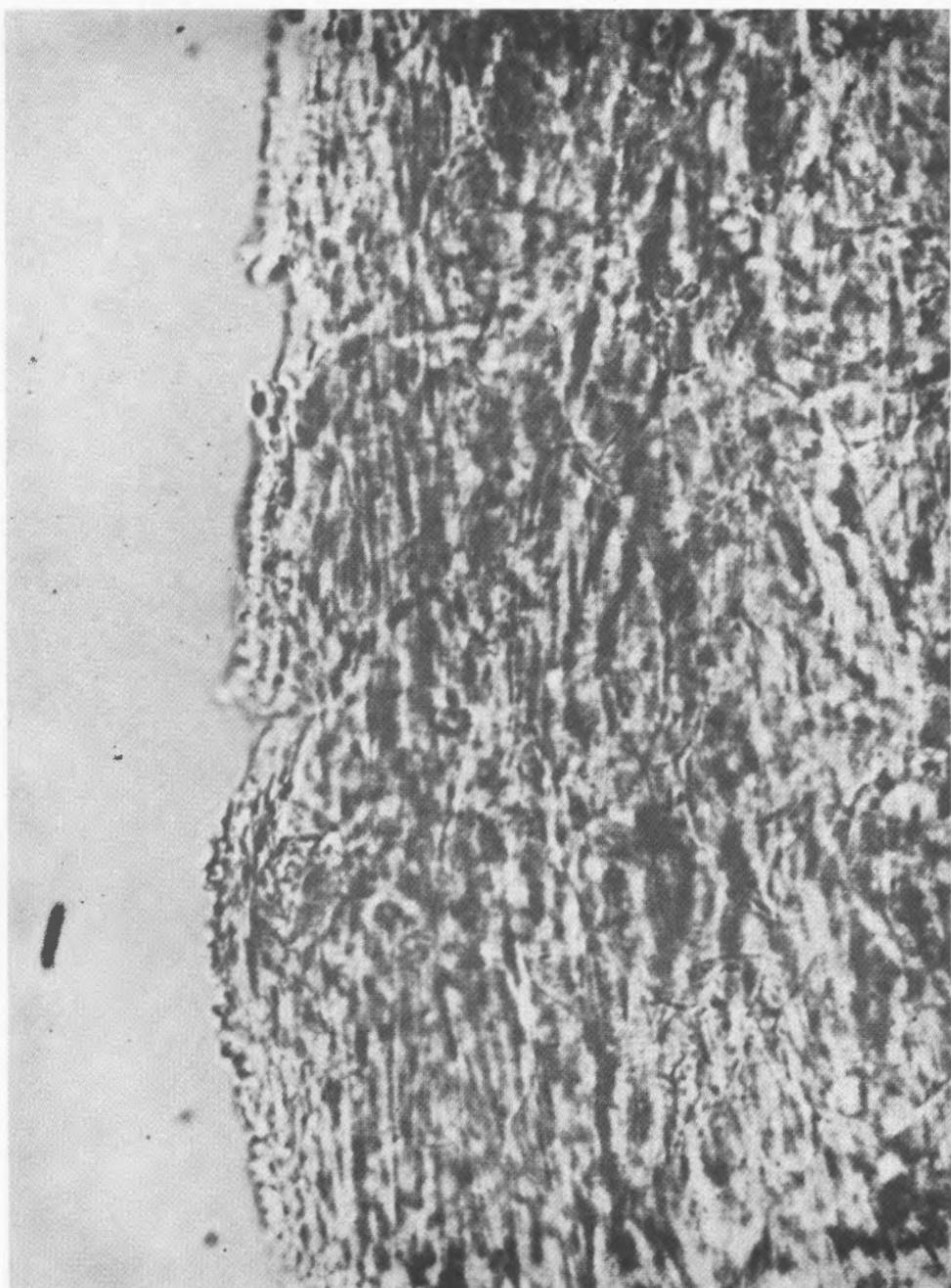


Plate 39



Plate 40

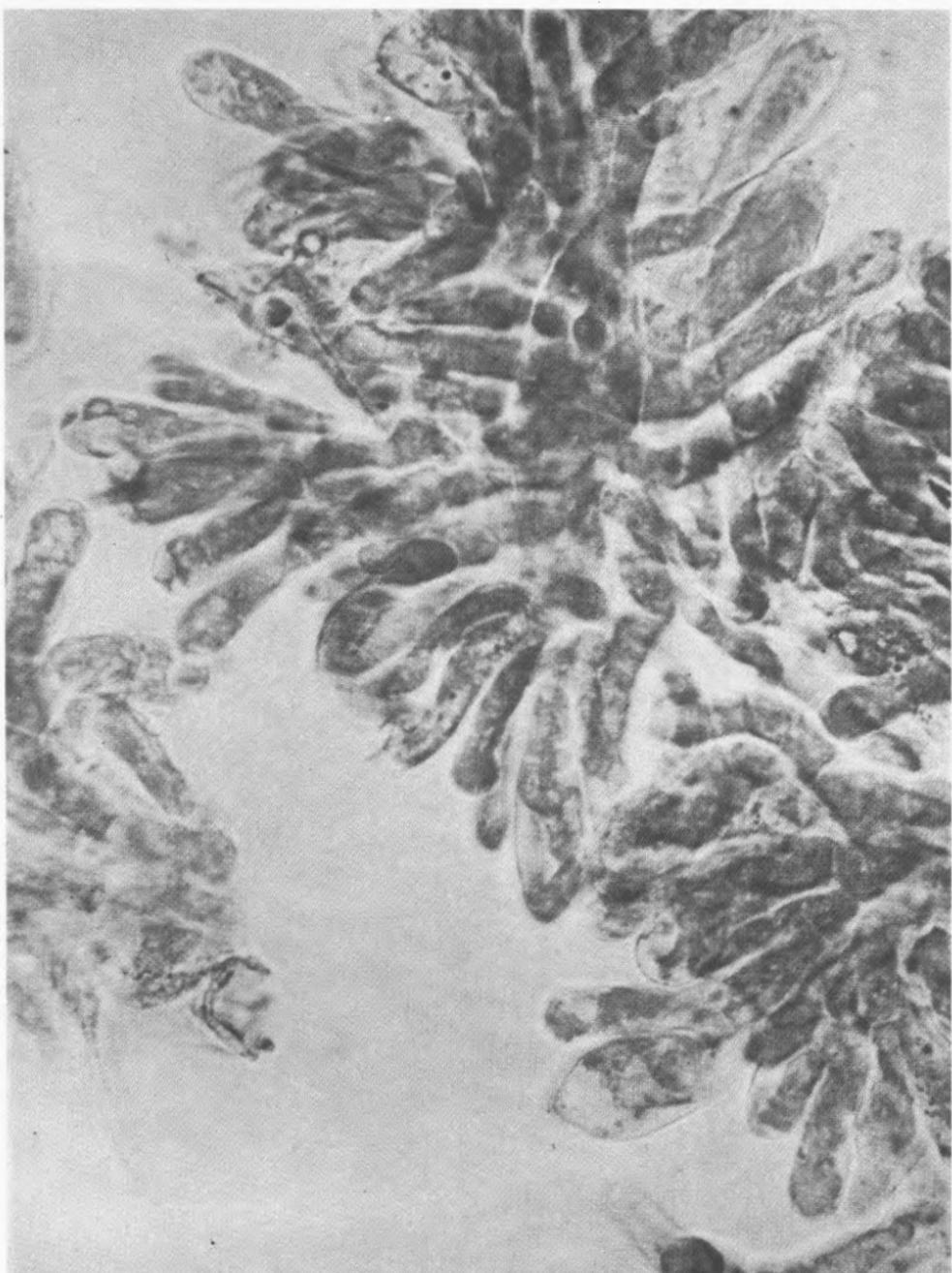


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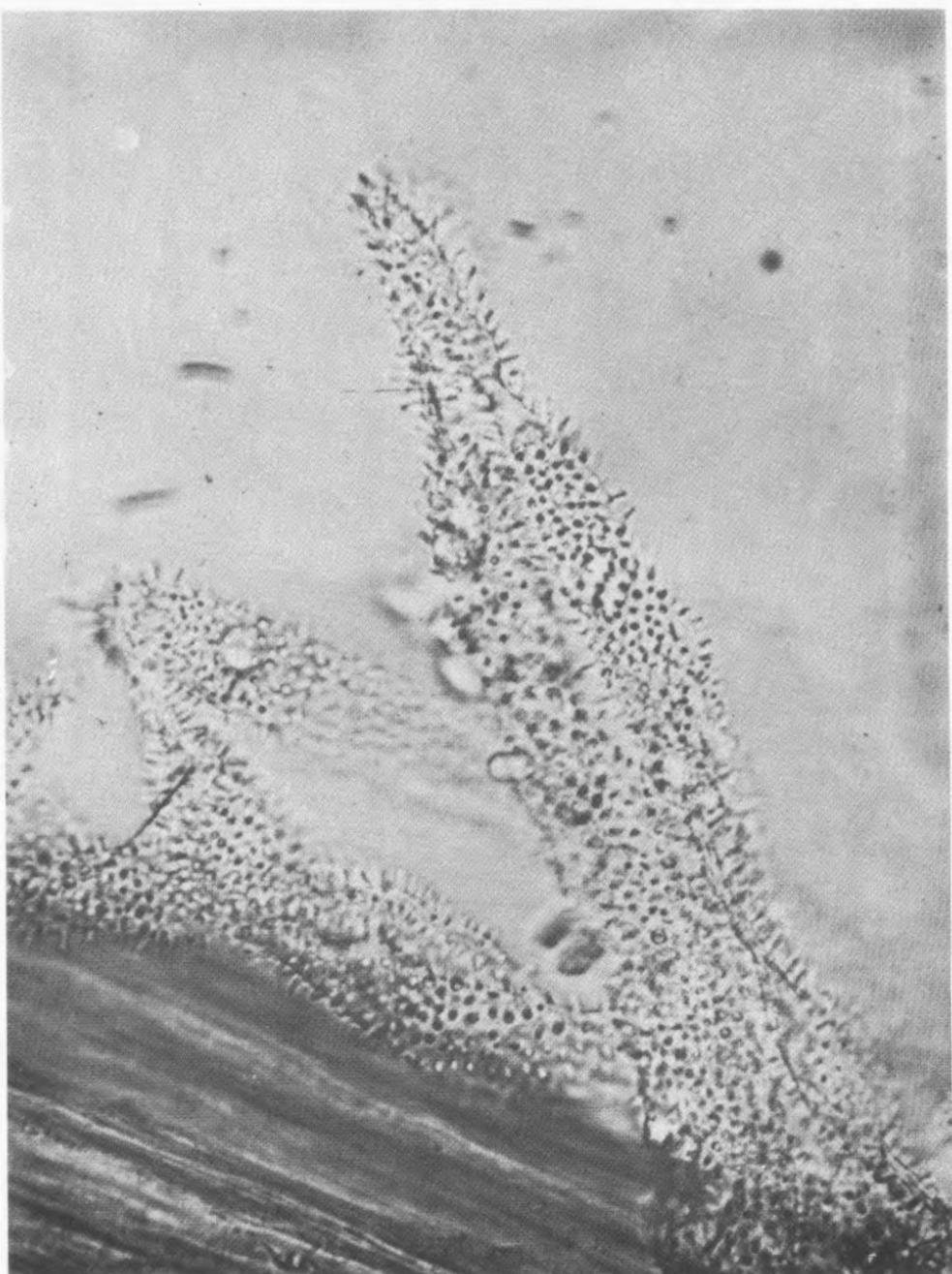


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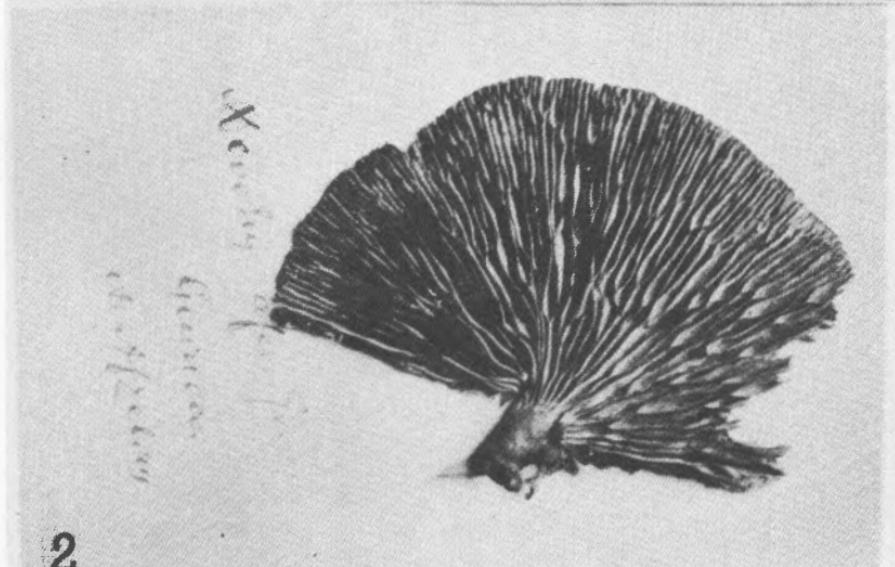
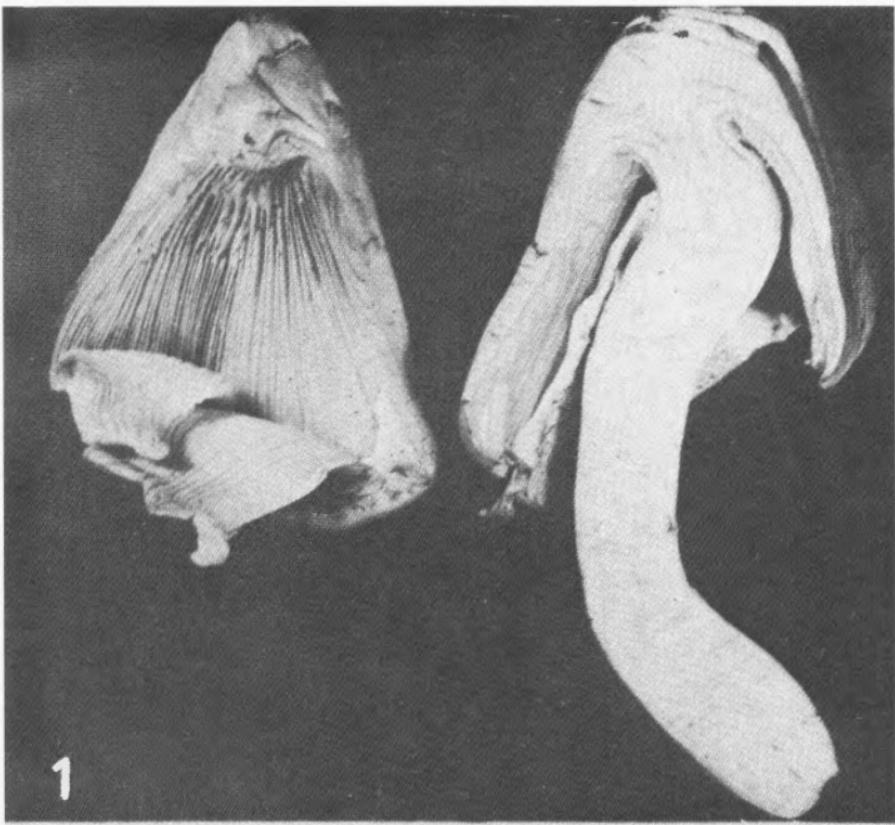


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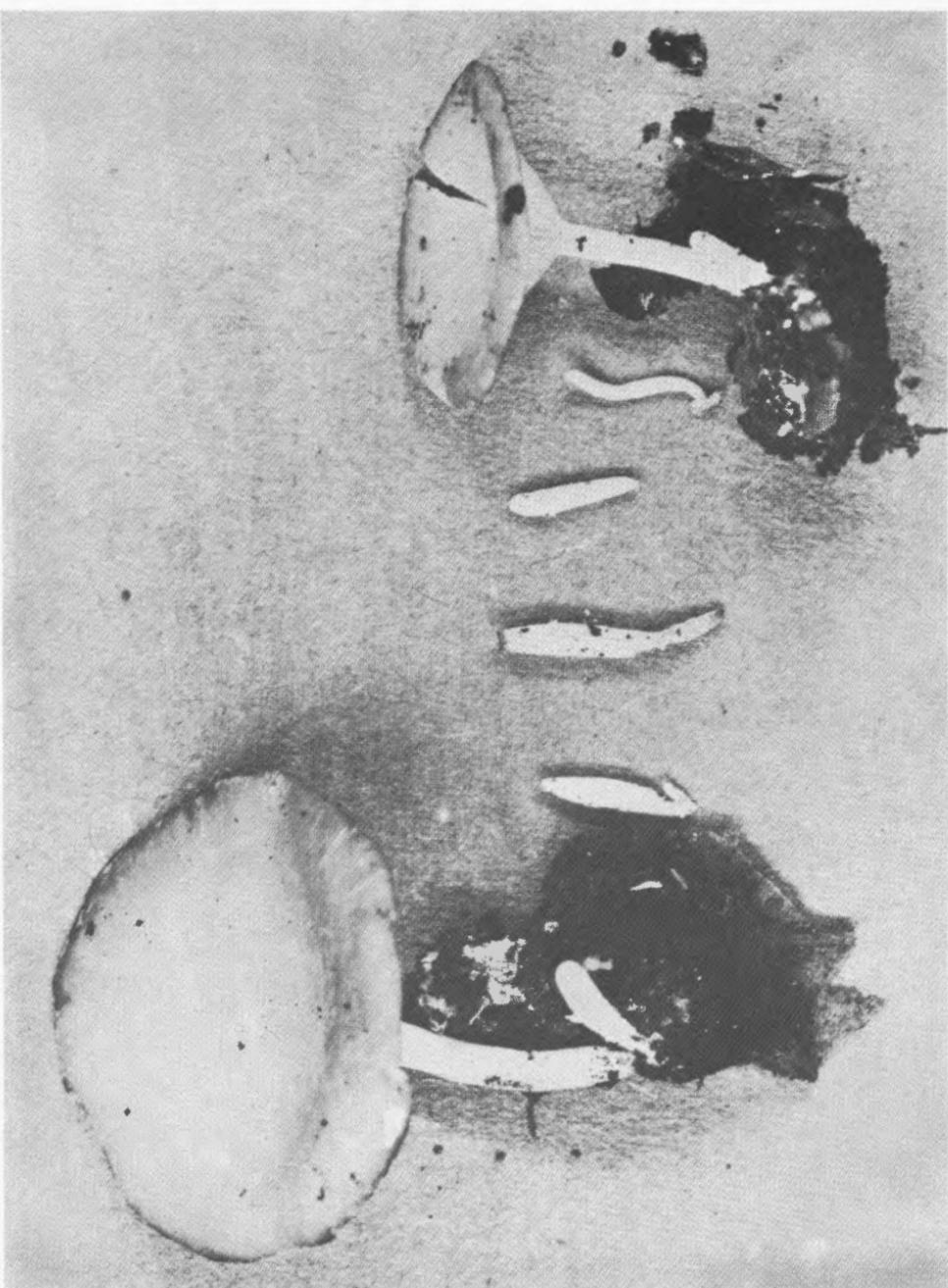


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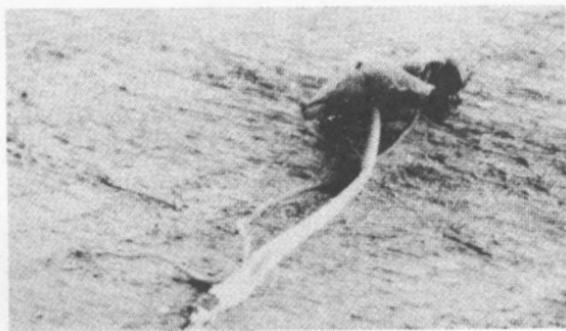


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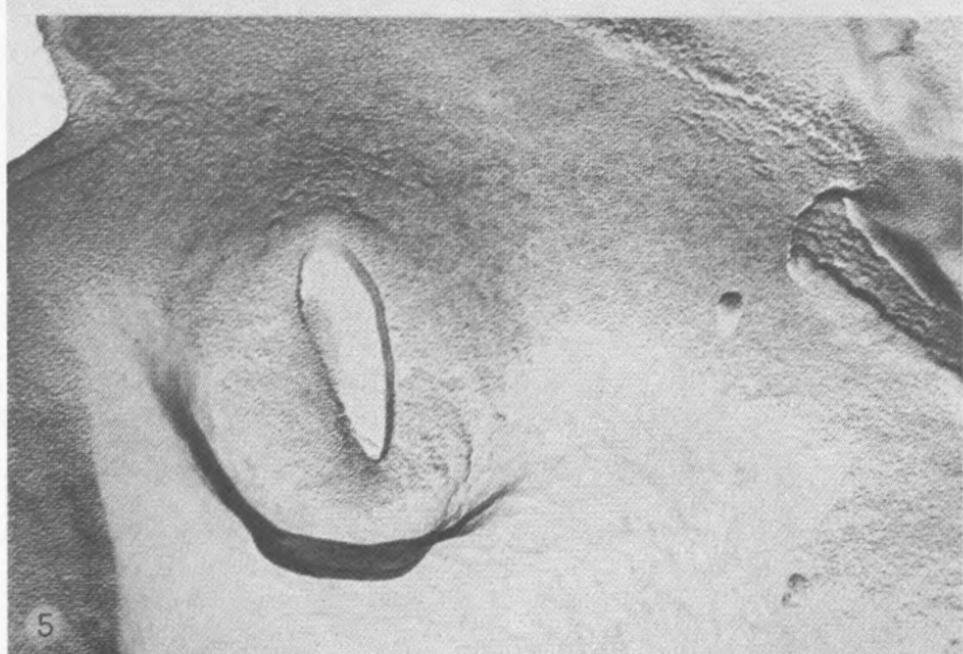
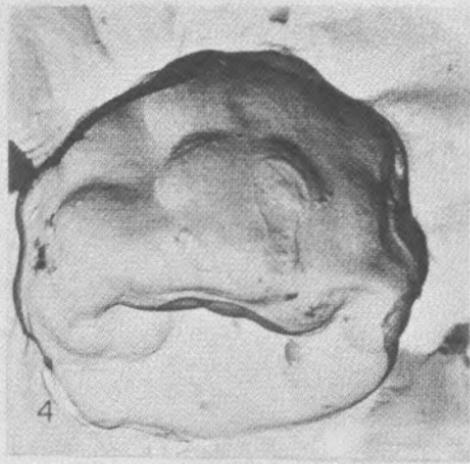
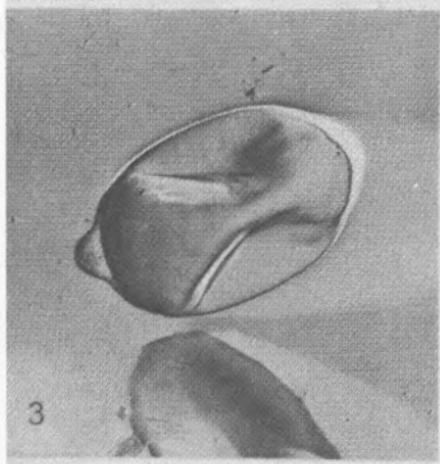
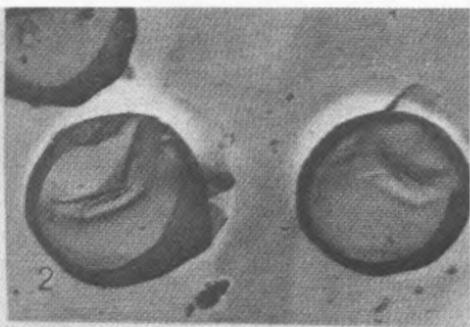
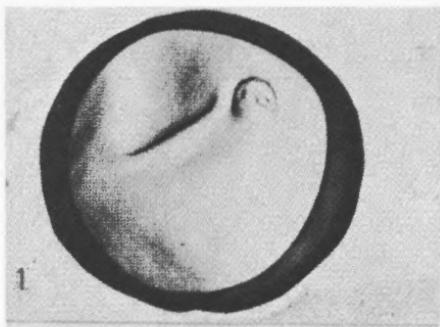


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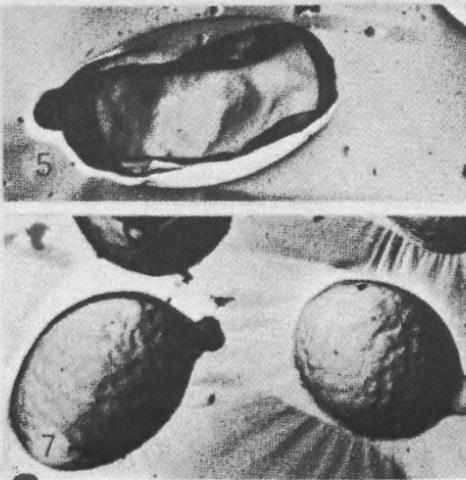
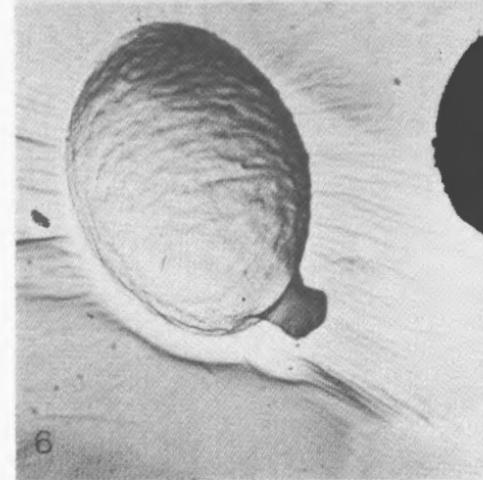
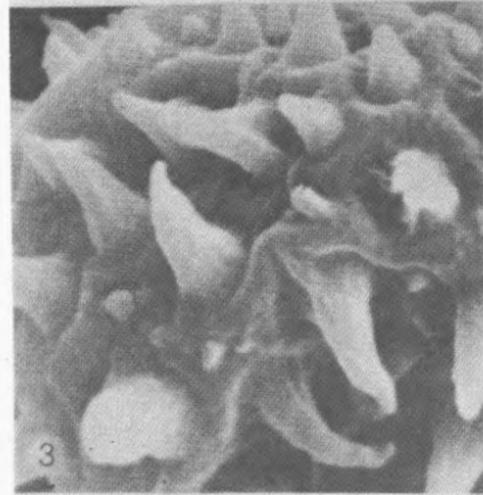
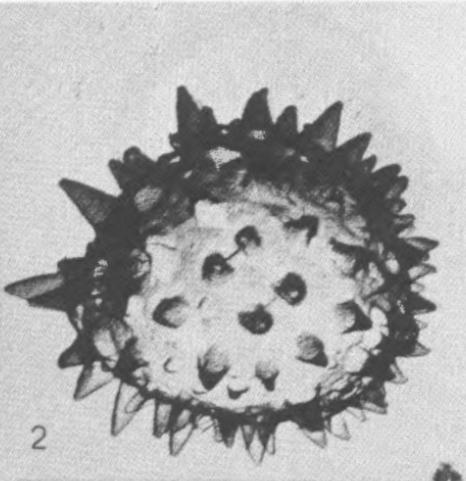
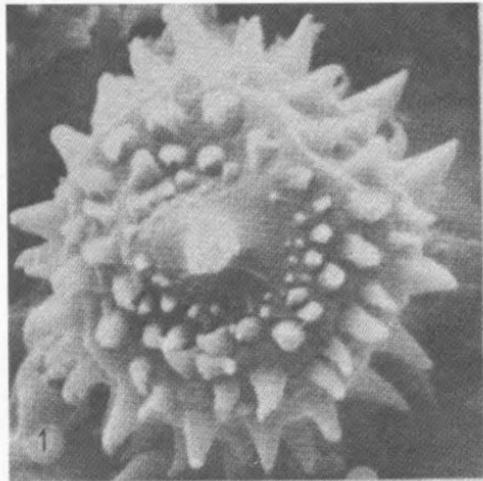


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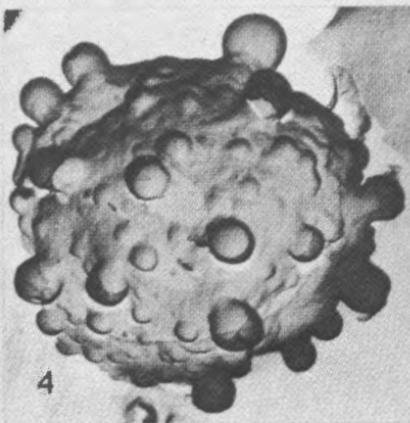
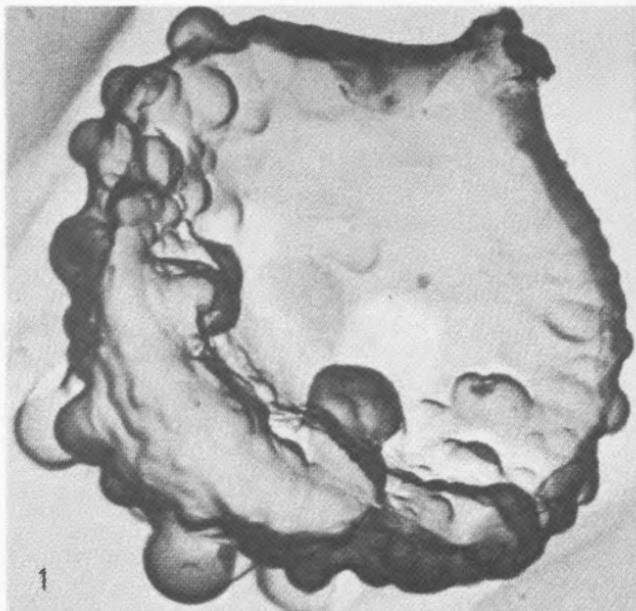
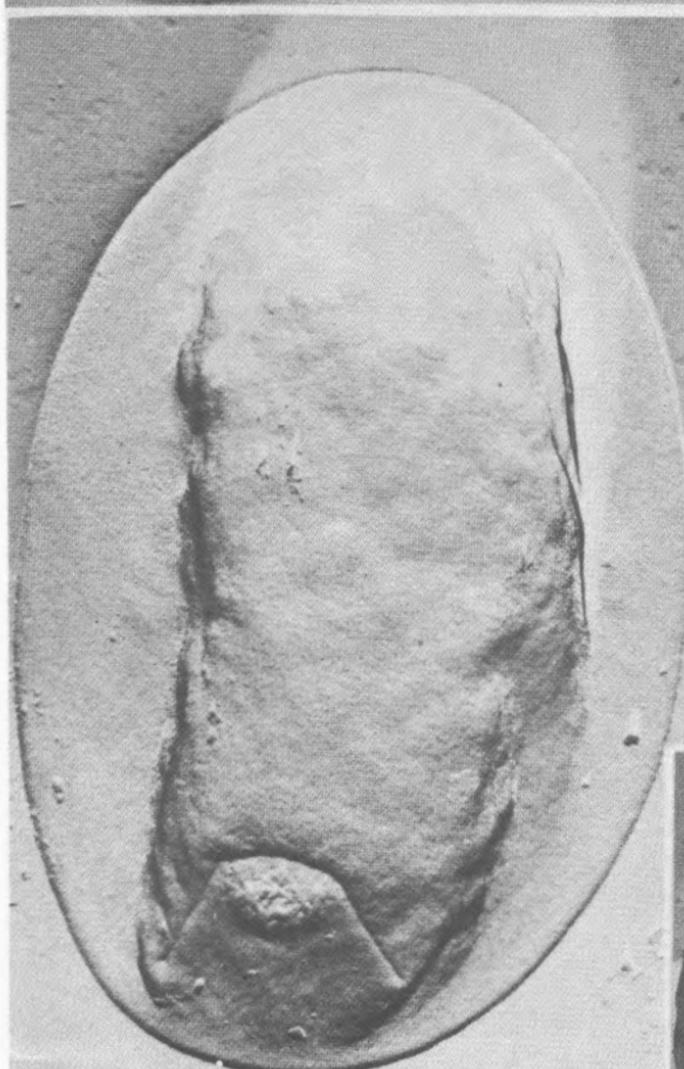
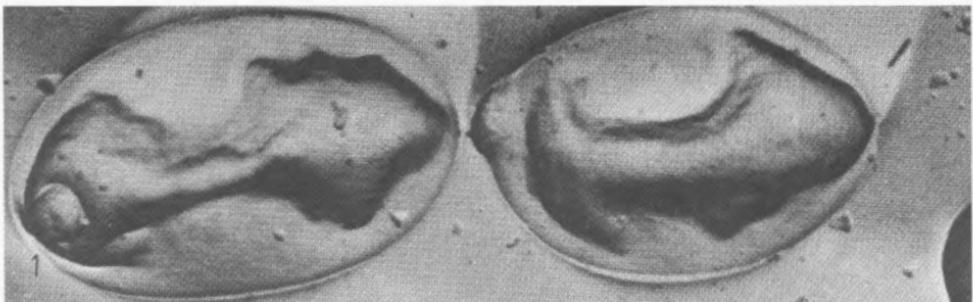


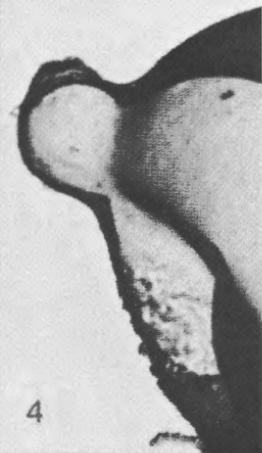
Plate 48



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Plate 49

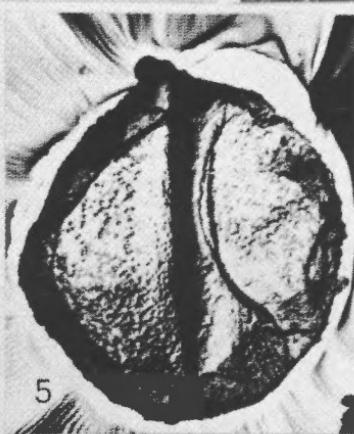
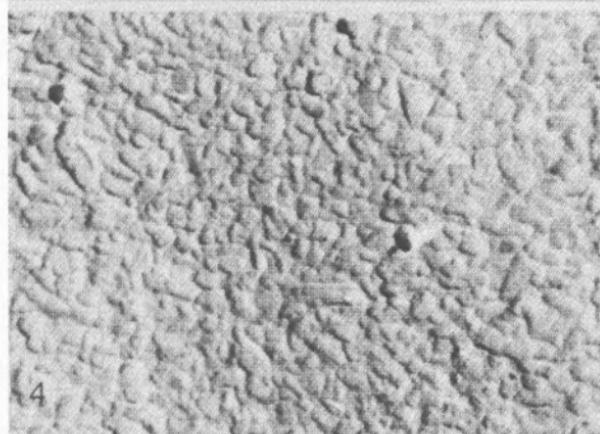
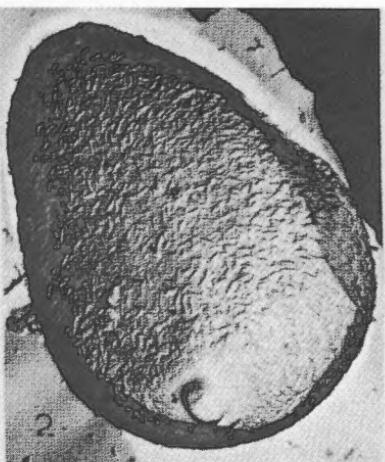
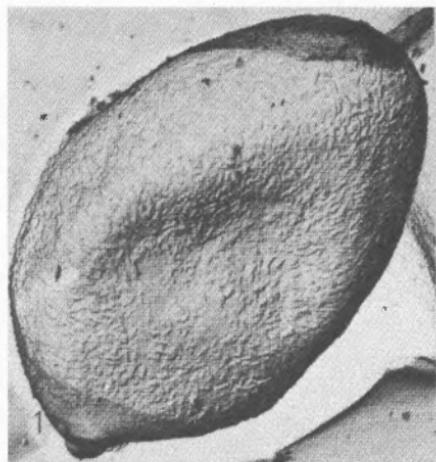


Plate 50

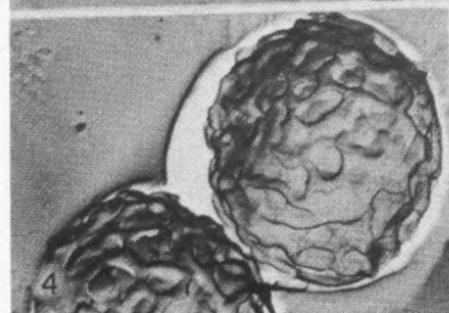
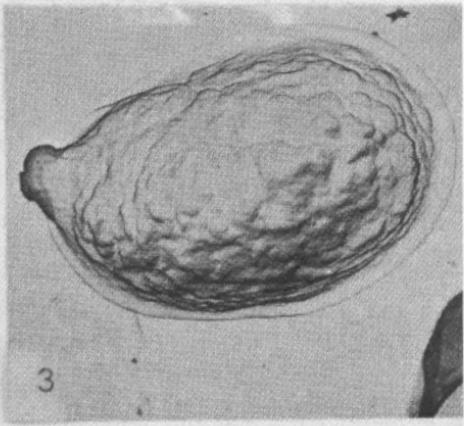
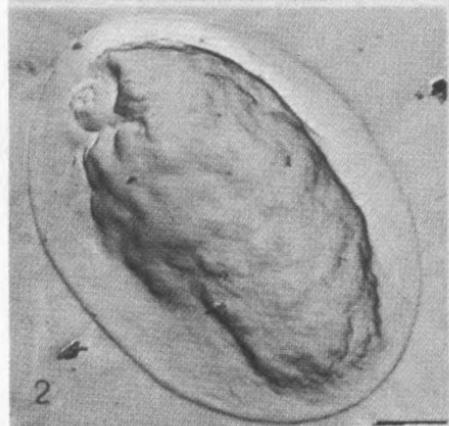
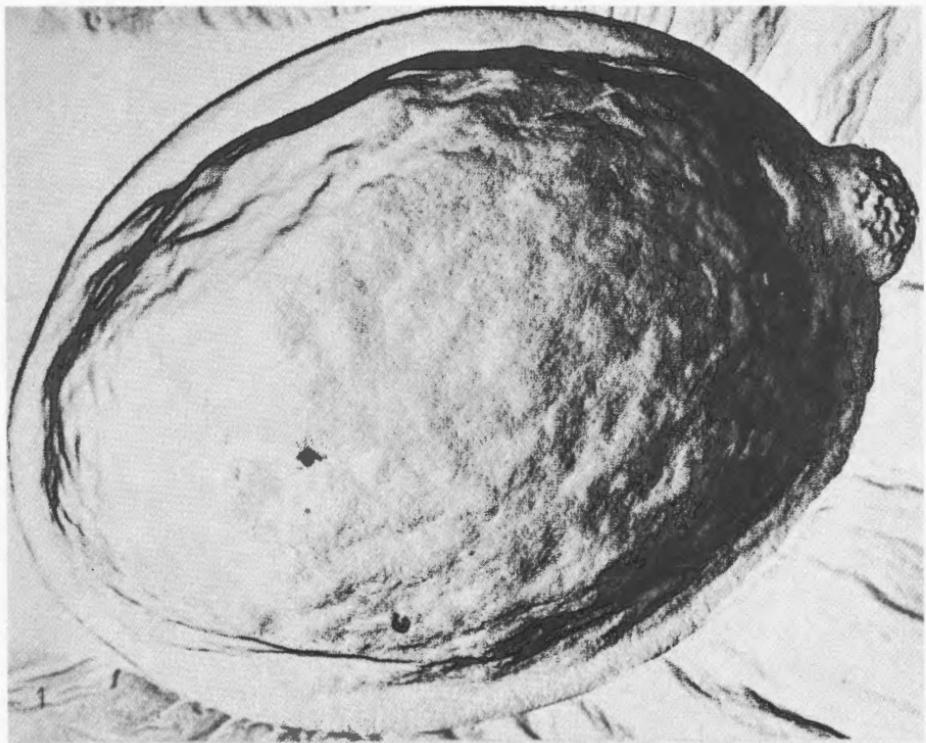


Plate 51

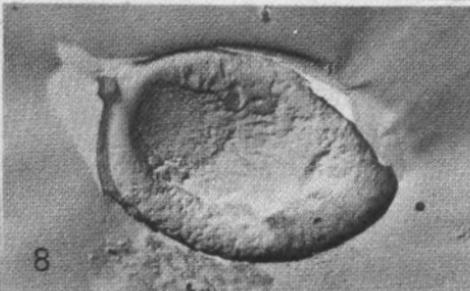
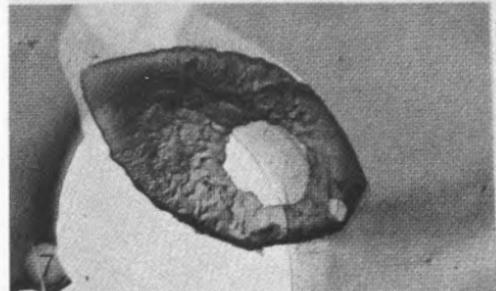
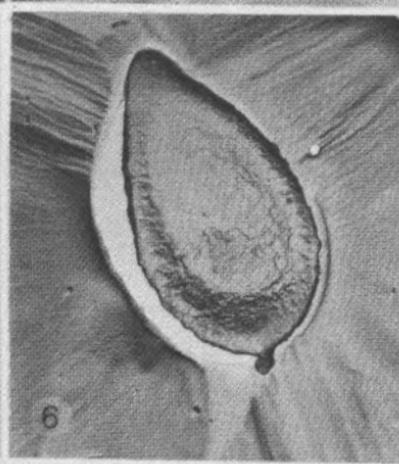
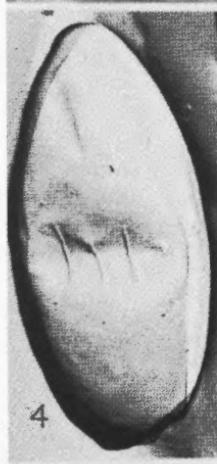
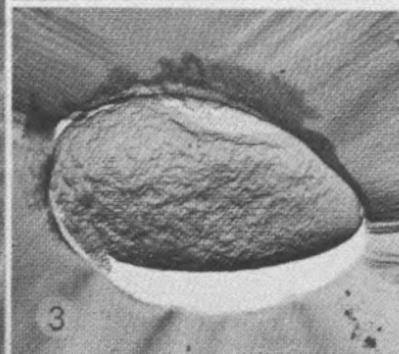
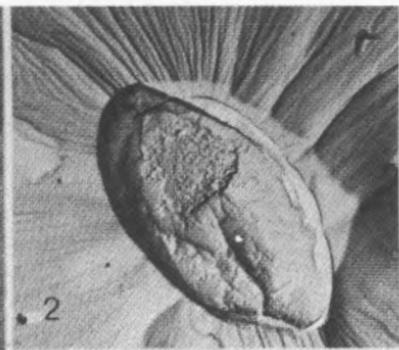
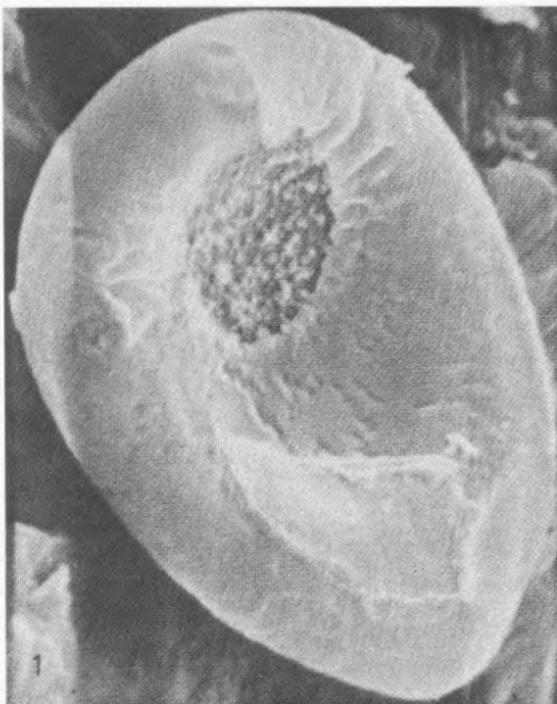
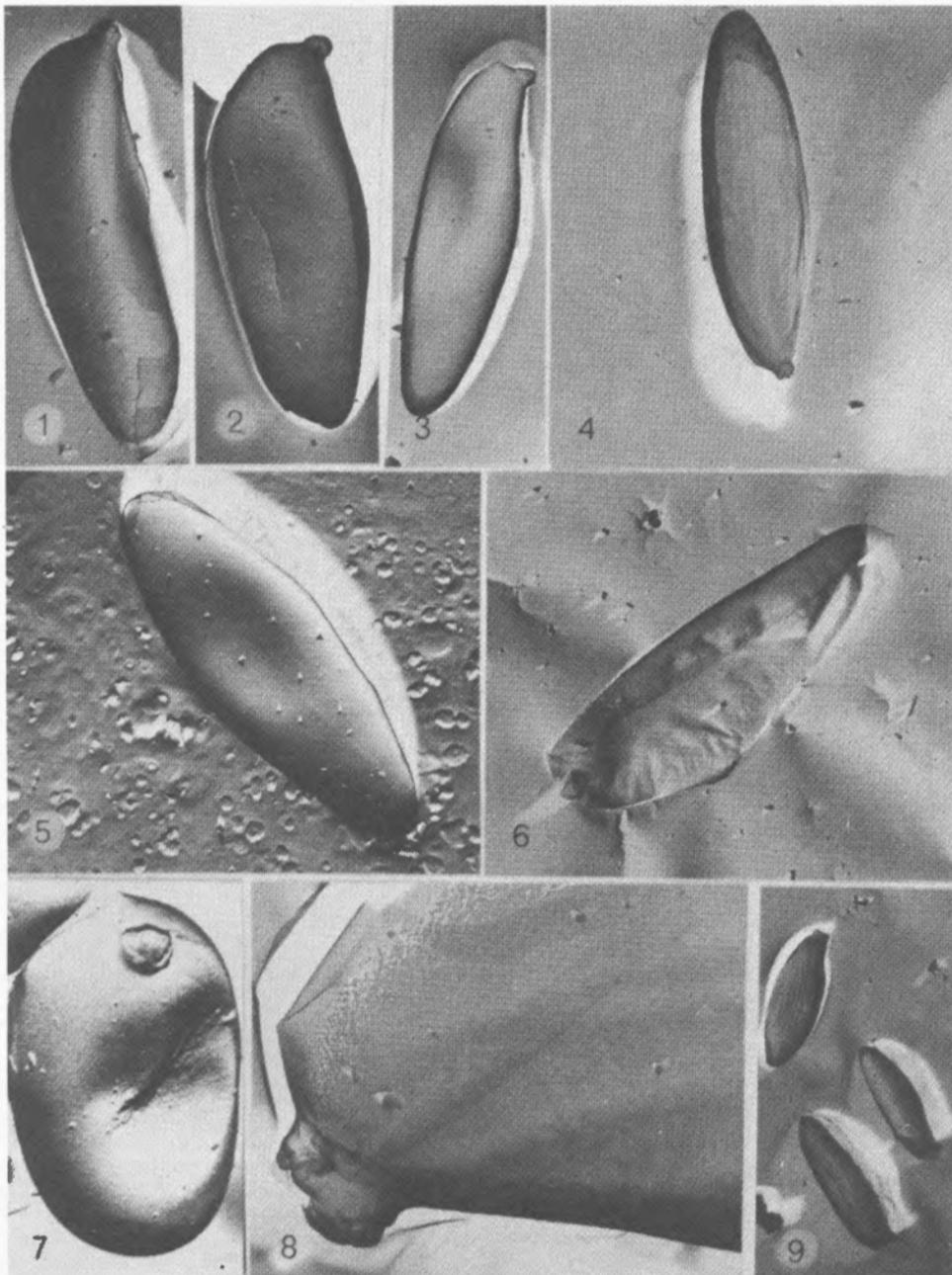
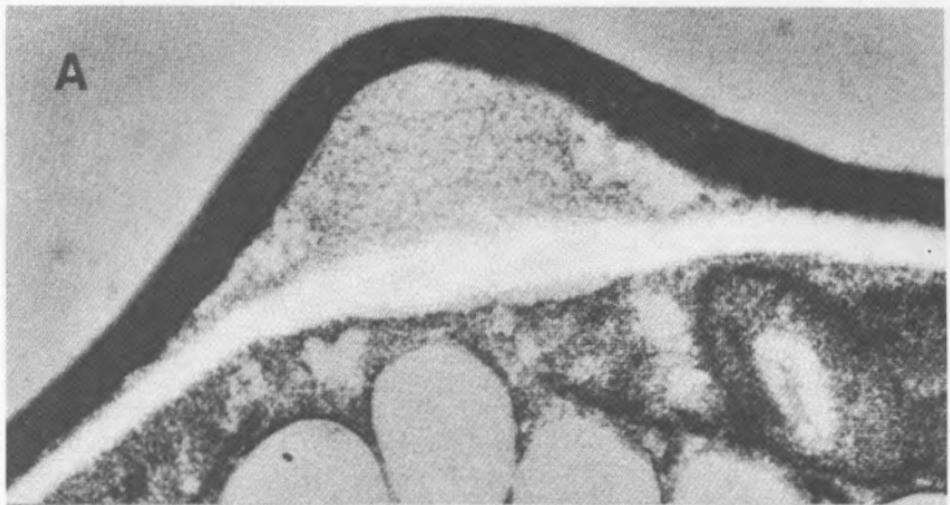


Plate 52



A



B



C

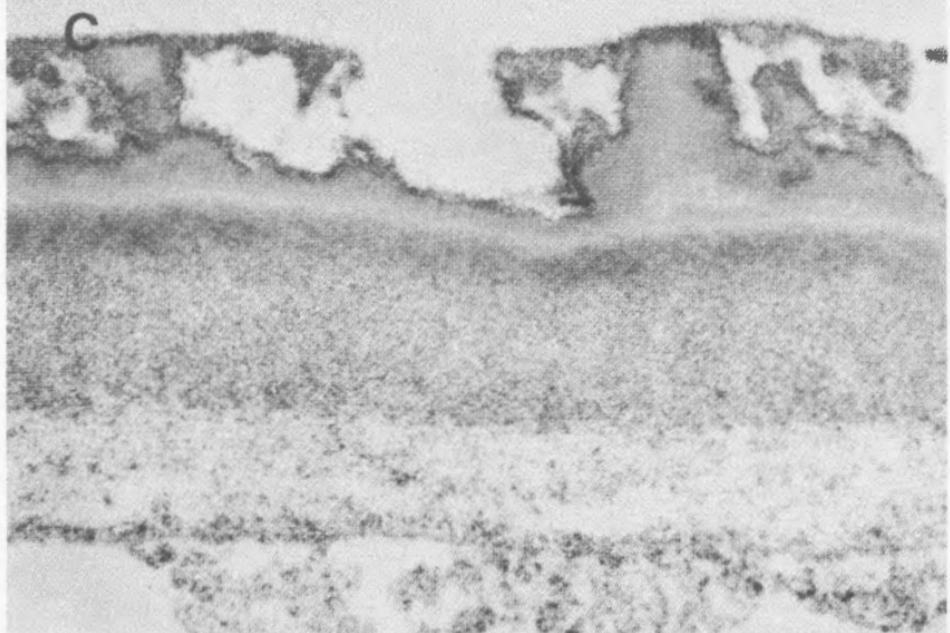


Plate 54



Plate 55

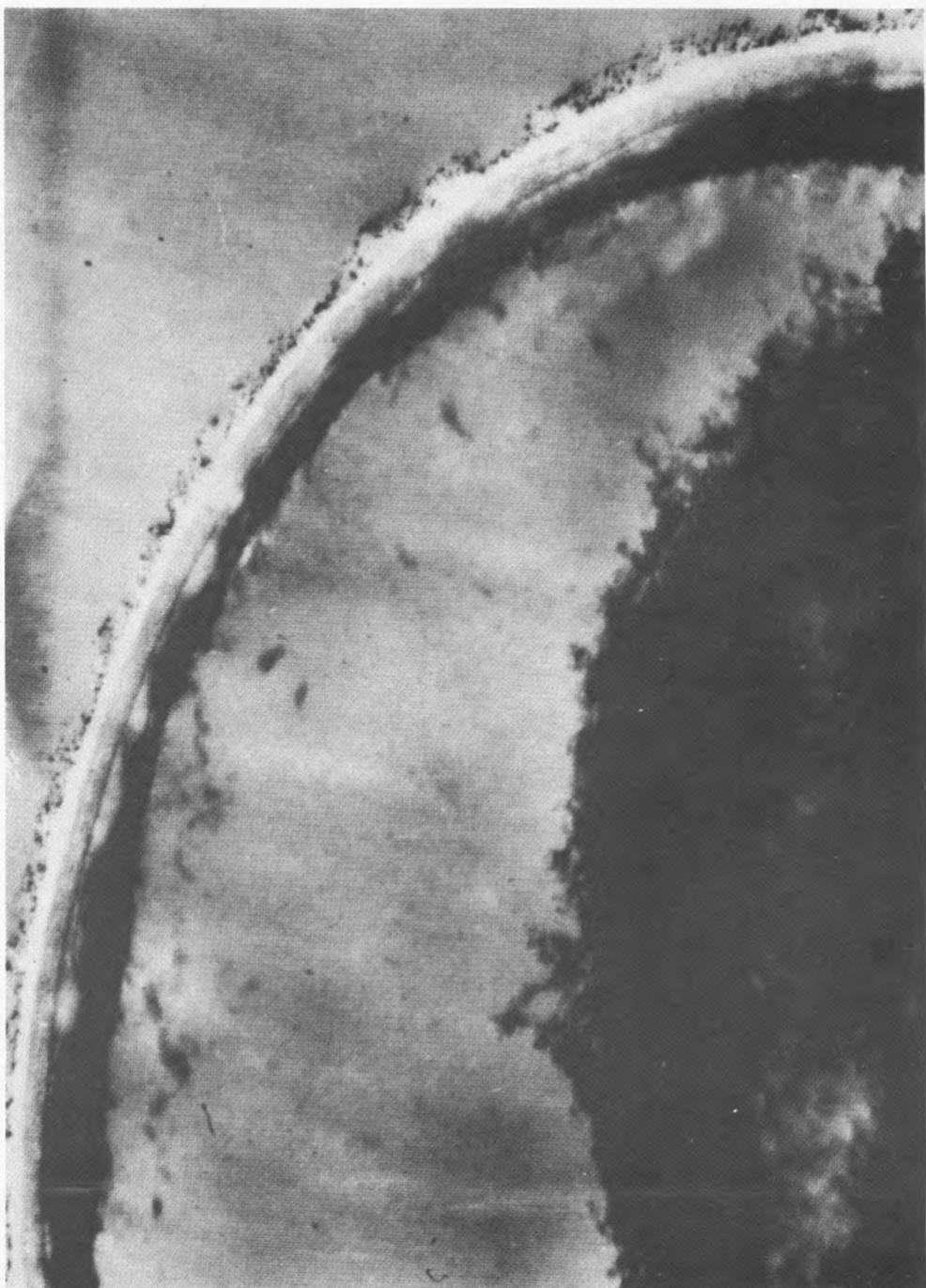


Plate 56

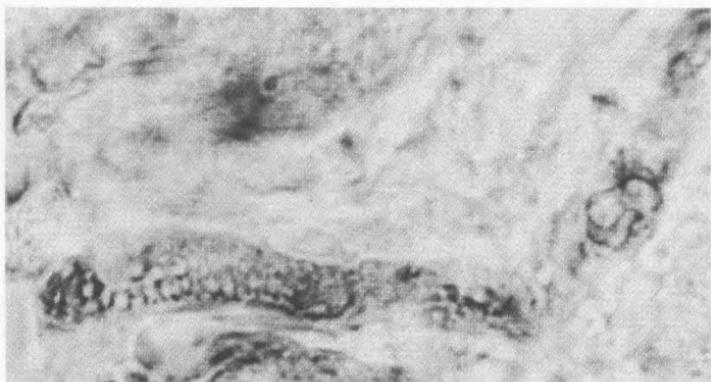
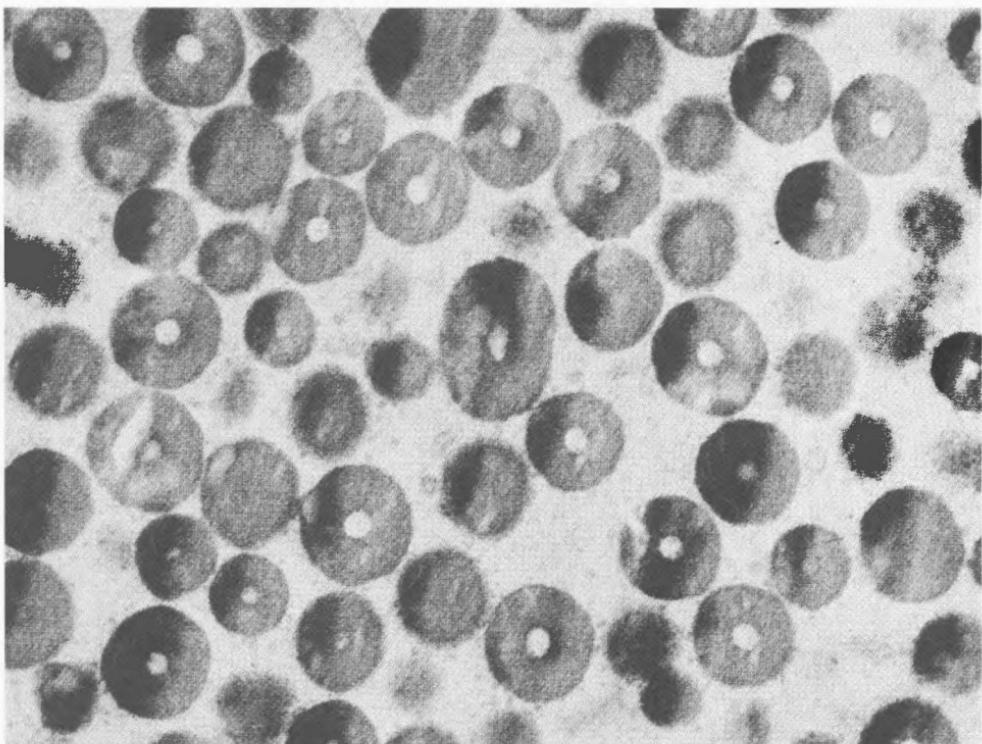
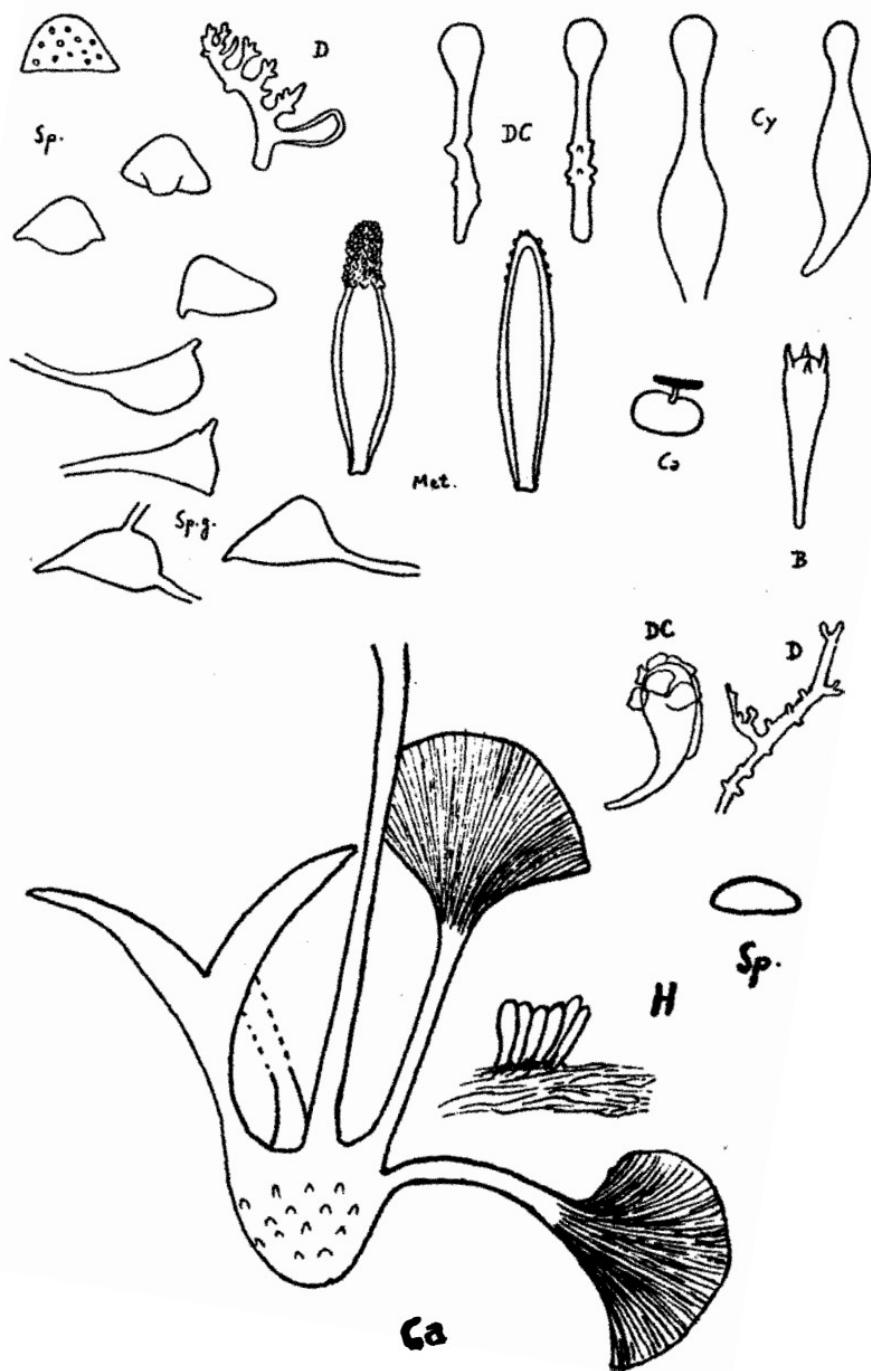


Plate 57



app.

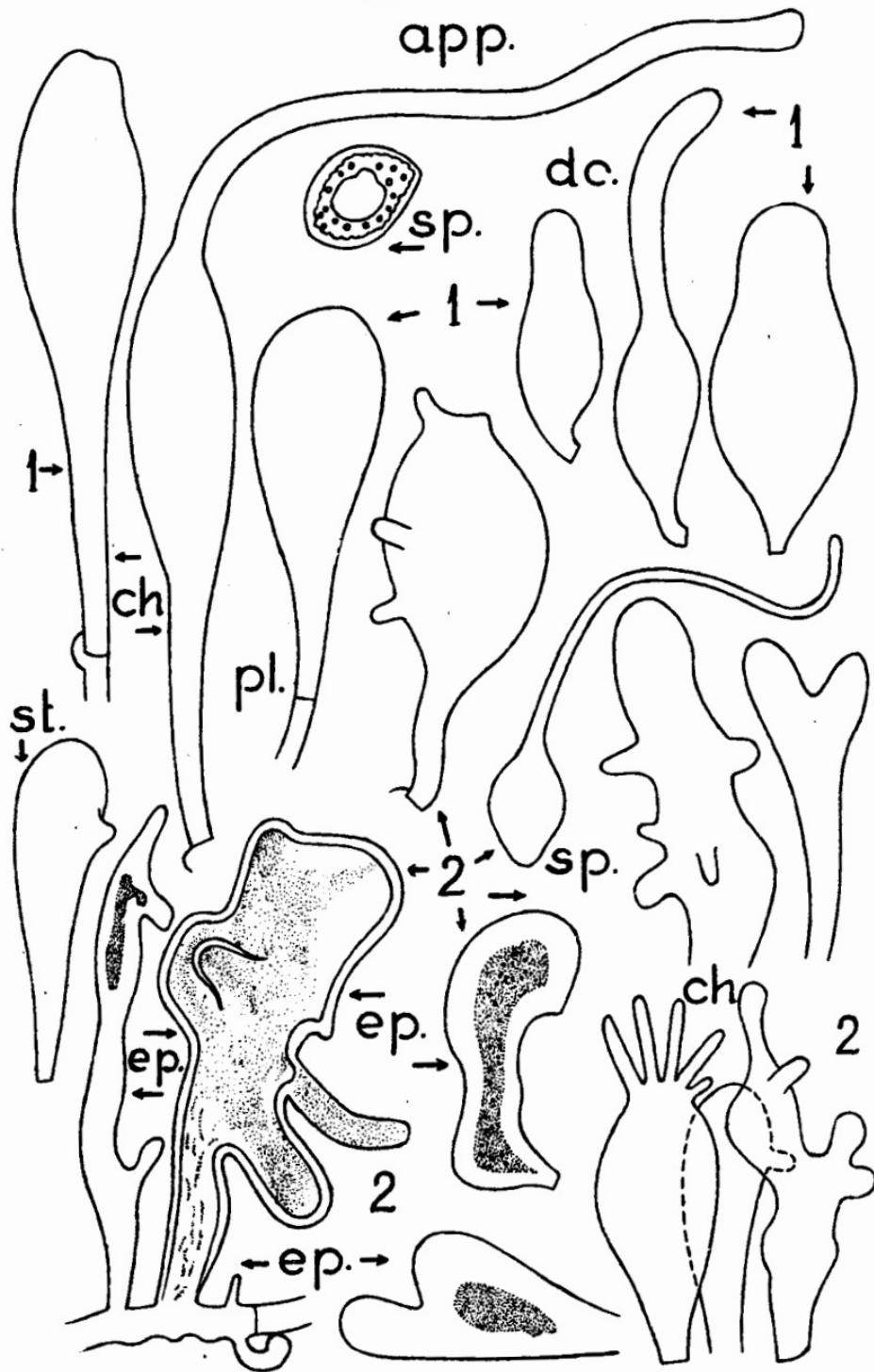
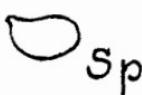


Plate 59

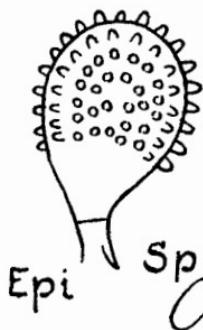


1

Epi



2



3

Epi

4



Hy



Epi

5



Epi

6



7



Epi

8

Sp

Plate 60

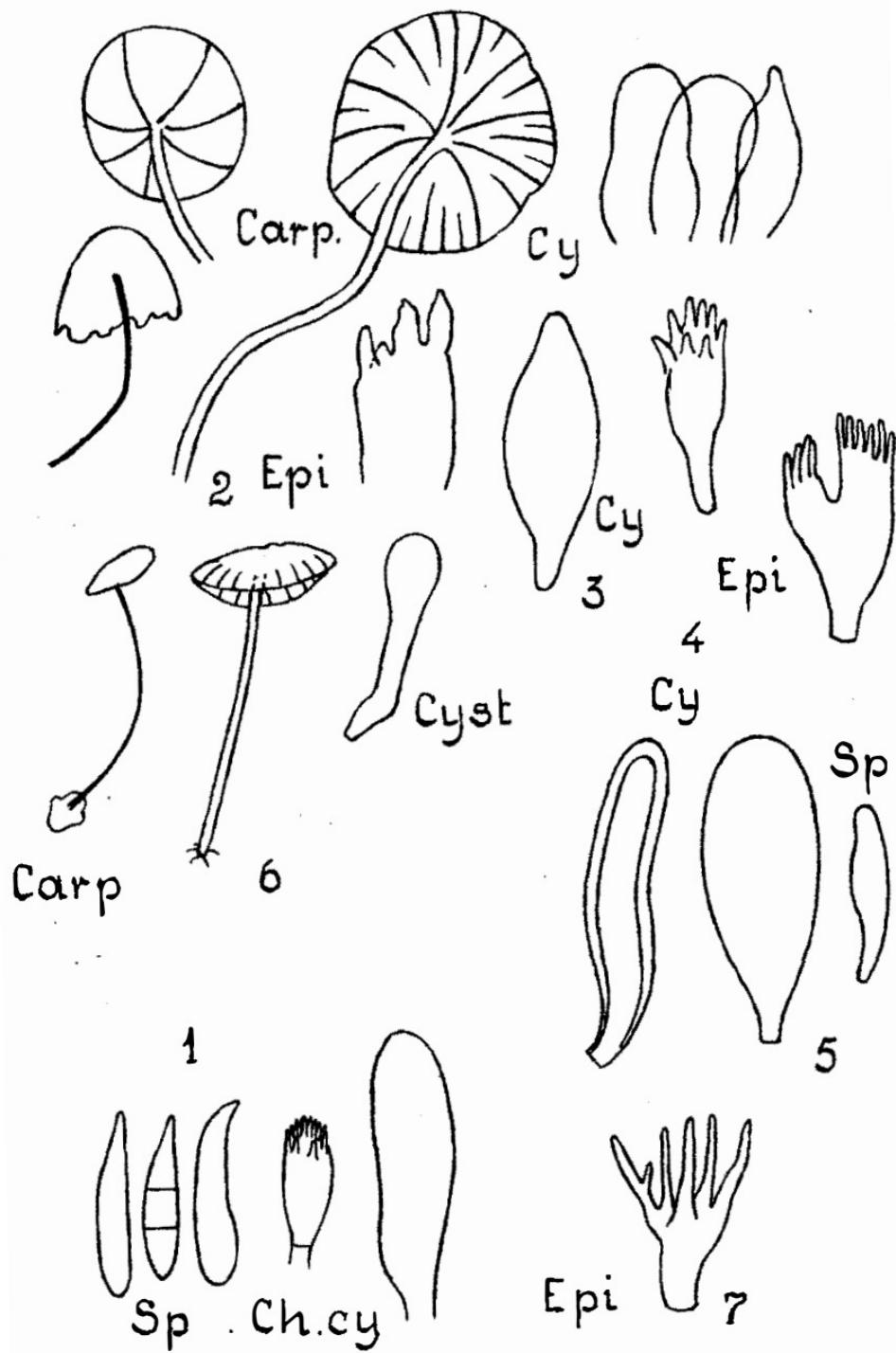


Plate 61

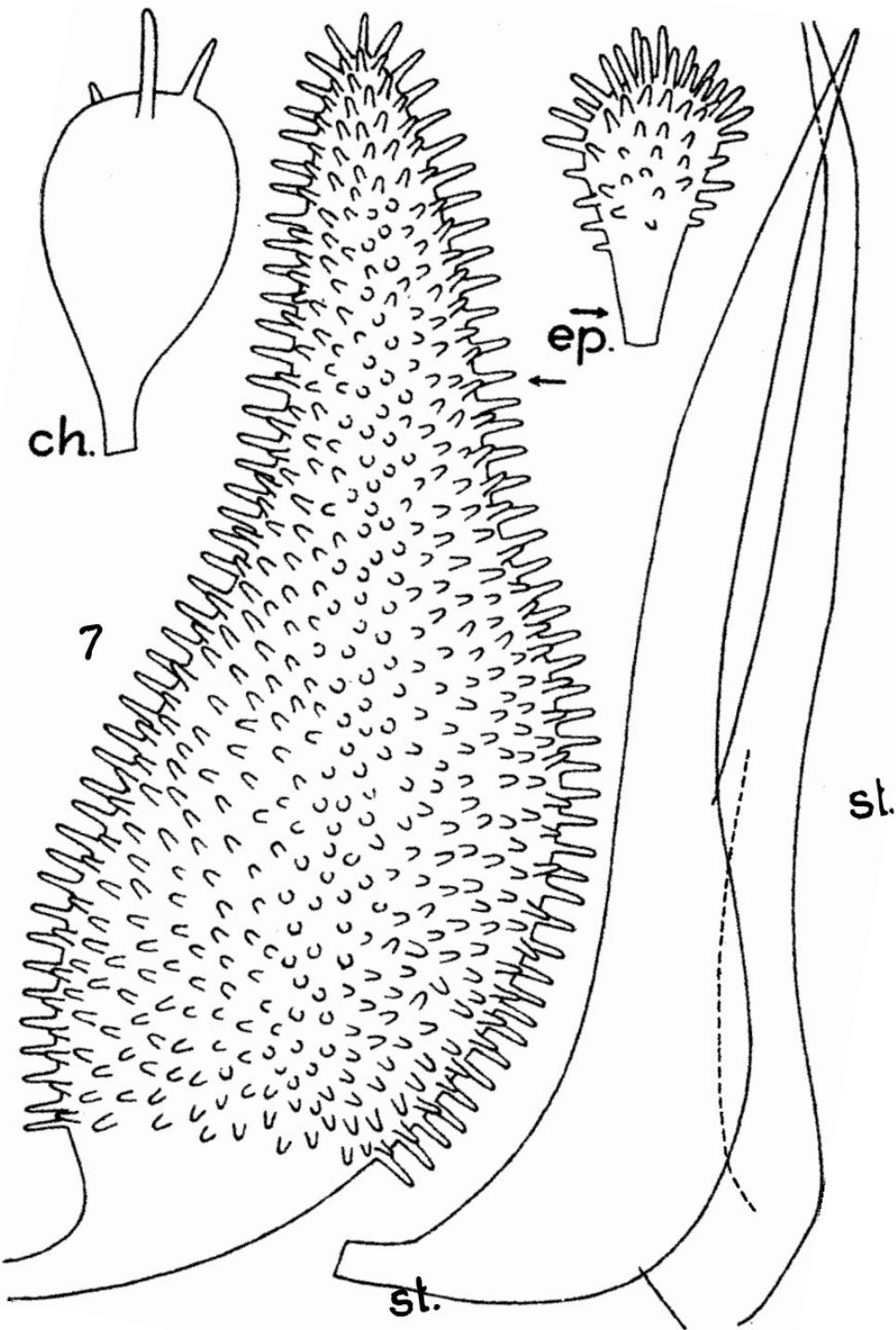


Plate 62

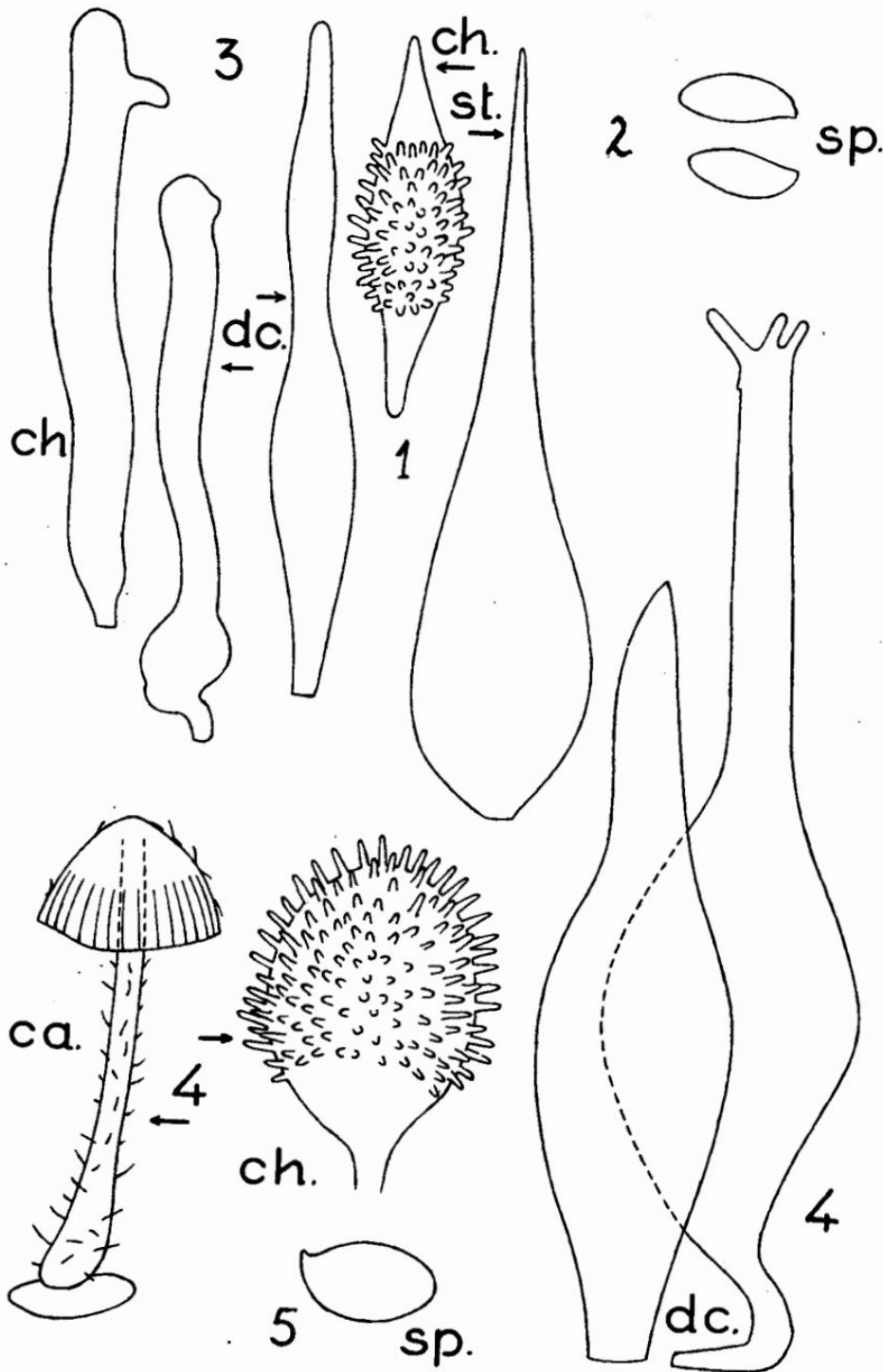


Plate 63

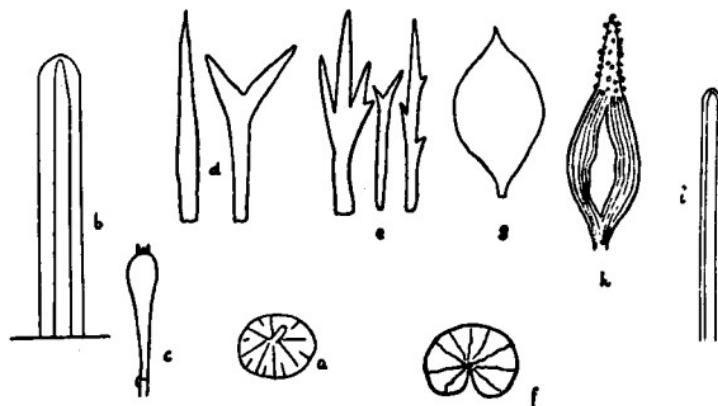
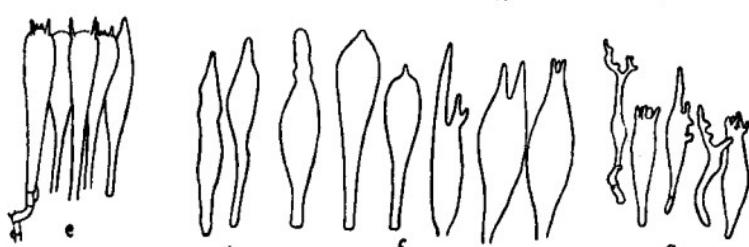
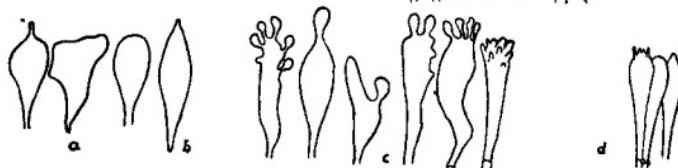
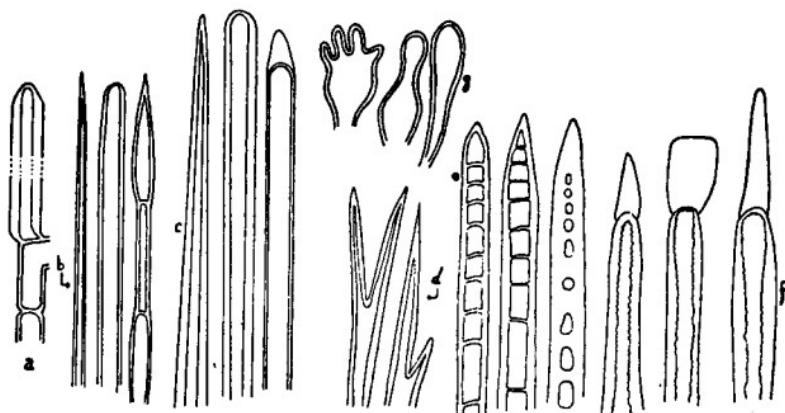
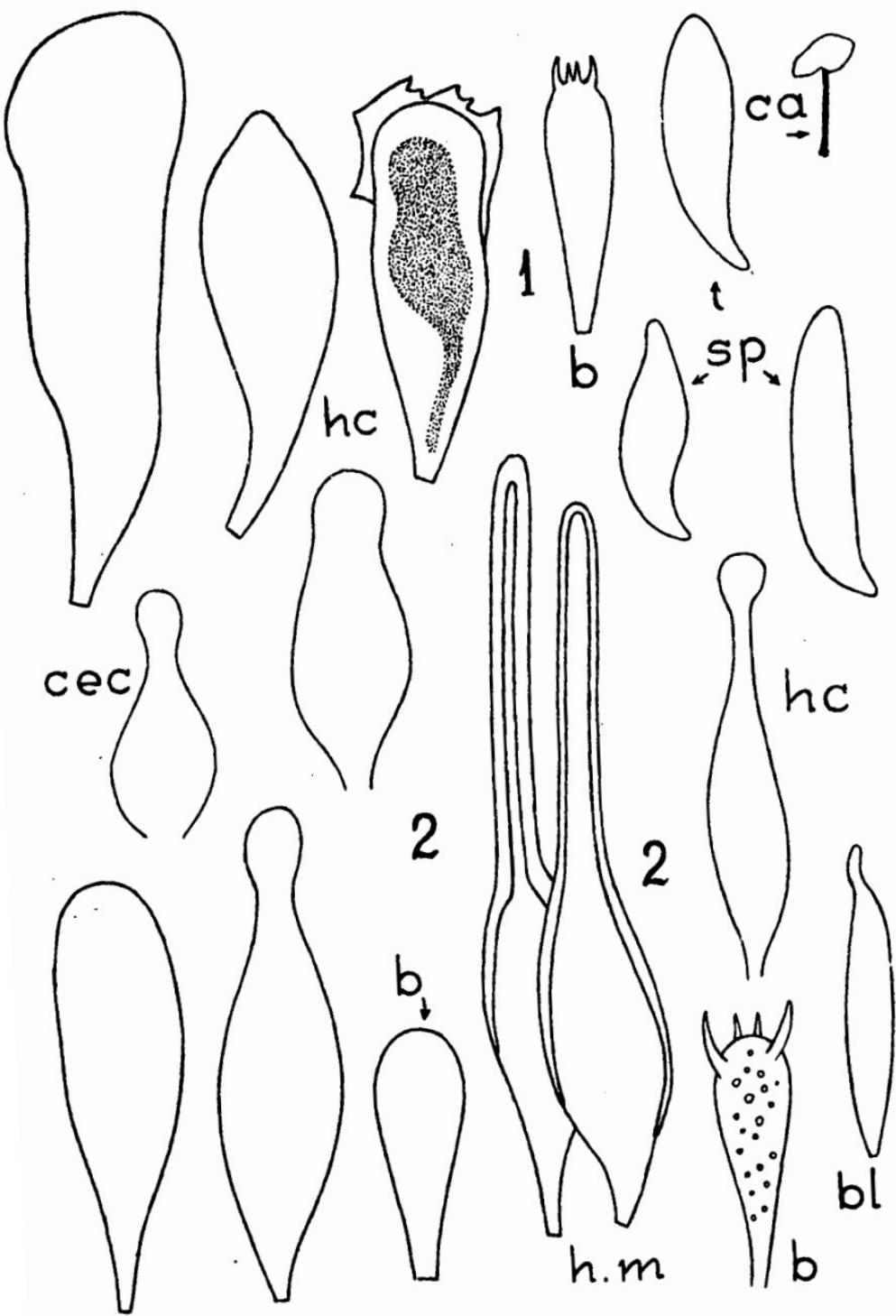


Plate 64



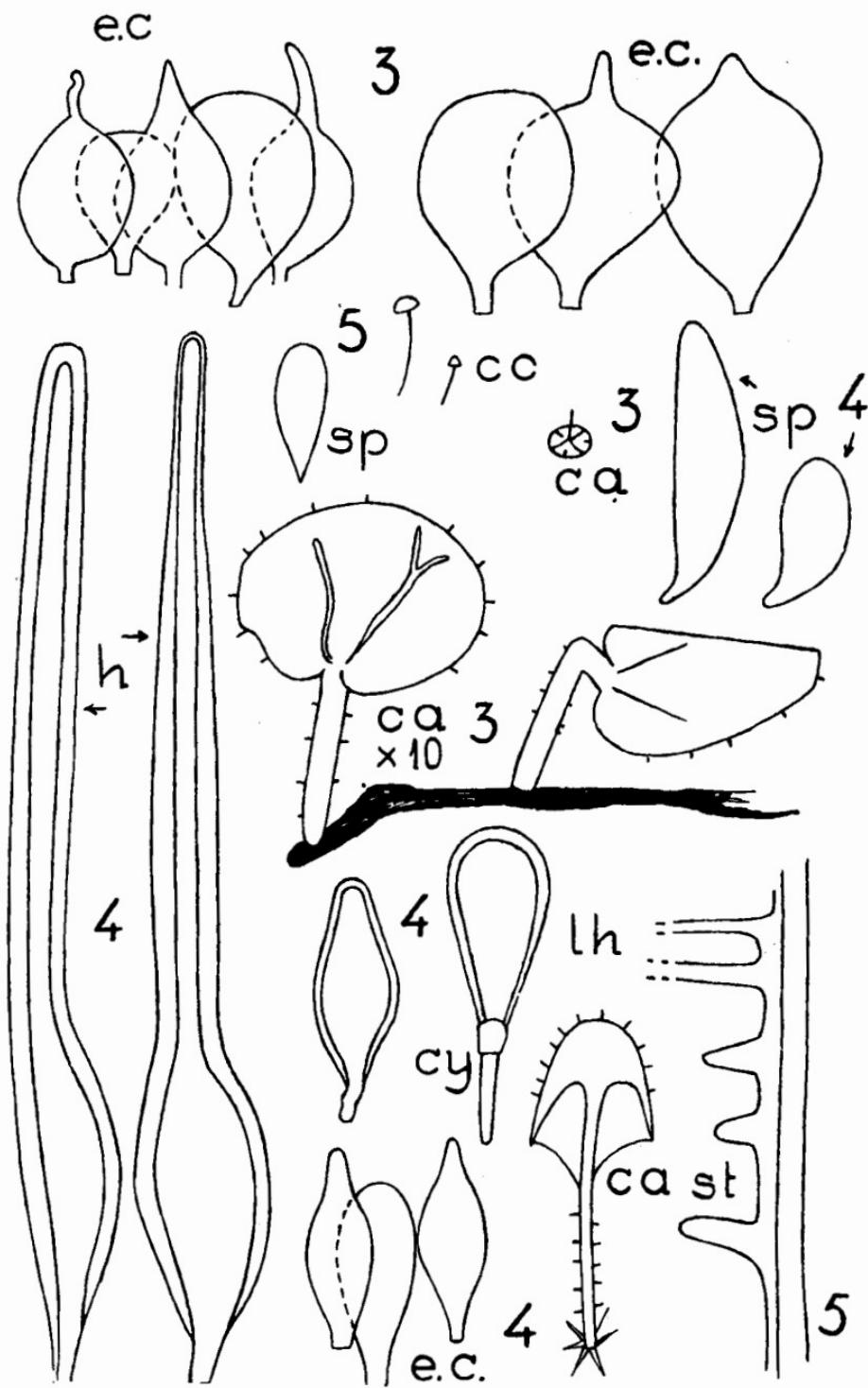


Plate 66

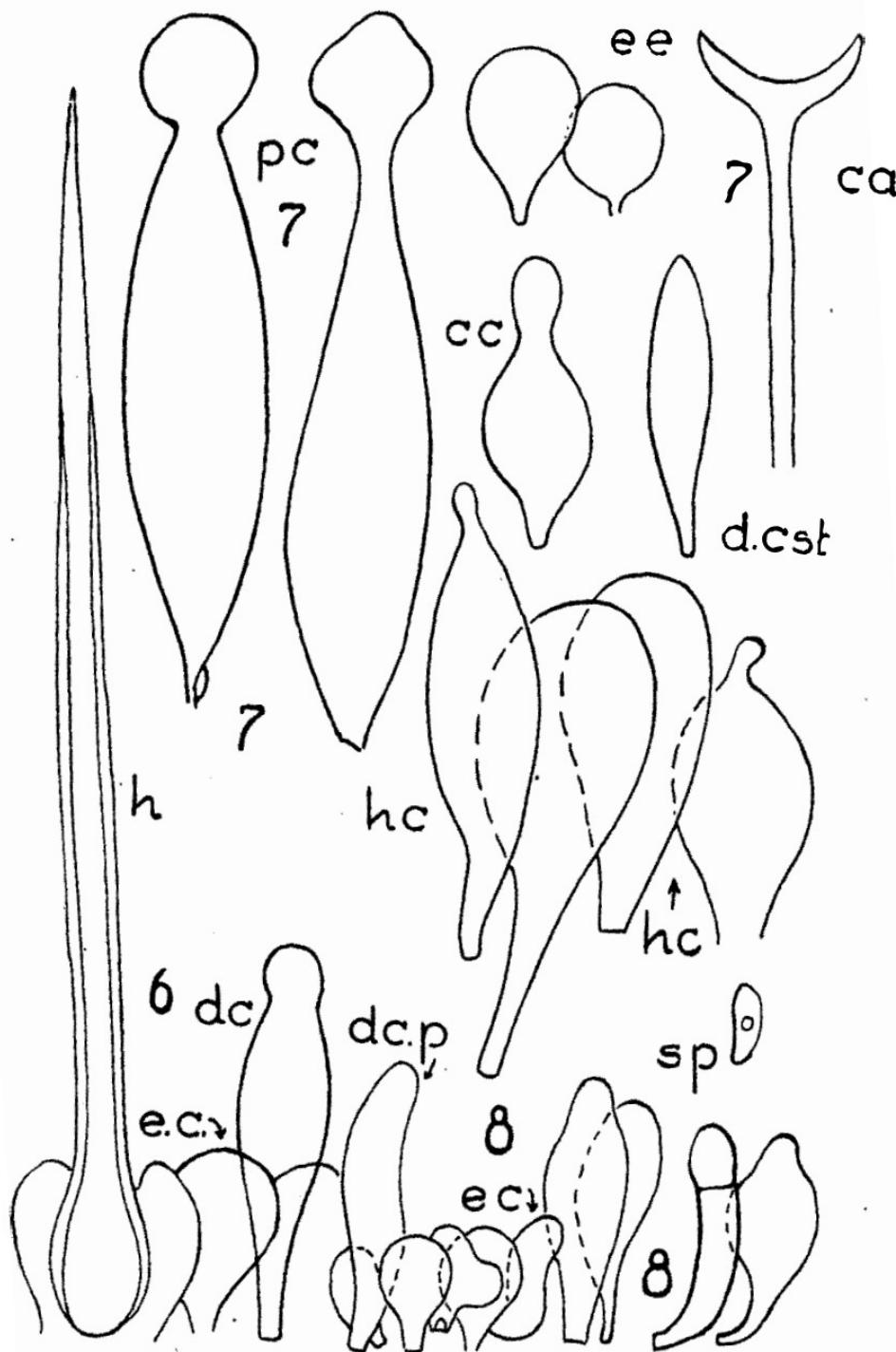


Plate 67

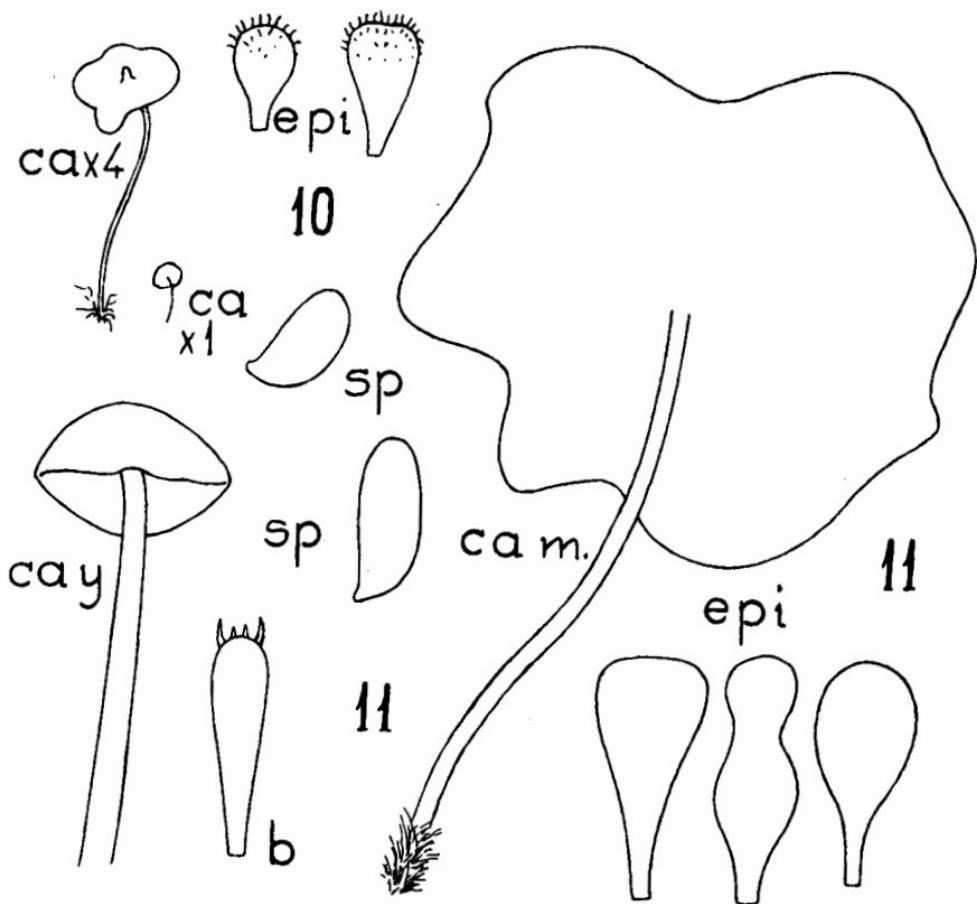
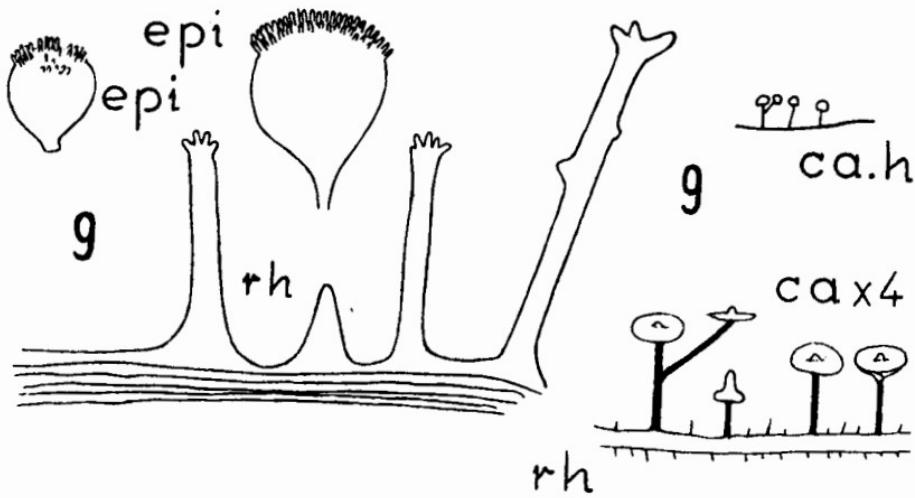


Plate 68

Fig.  
A

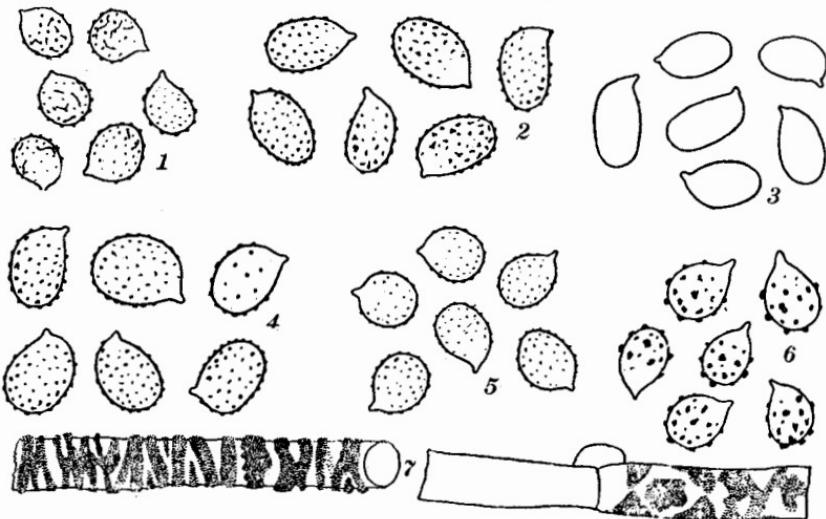


Fig.  
B.

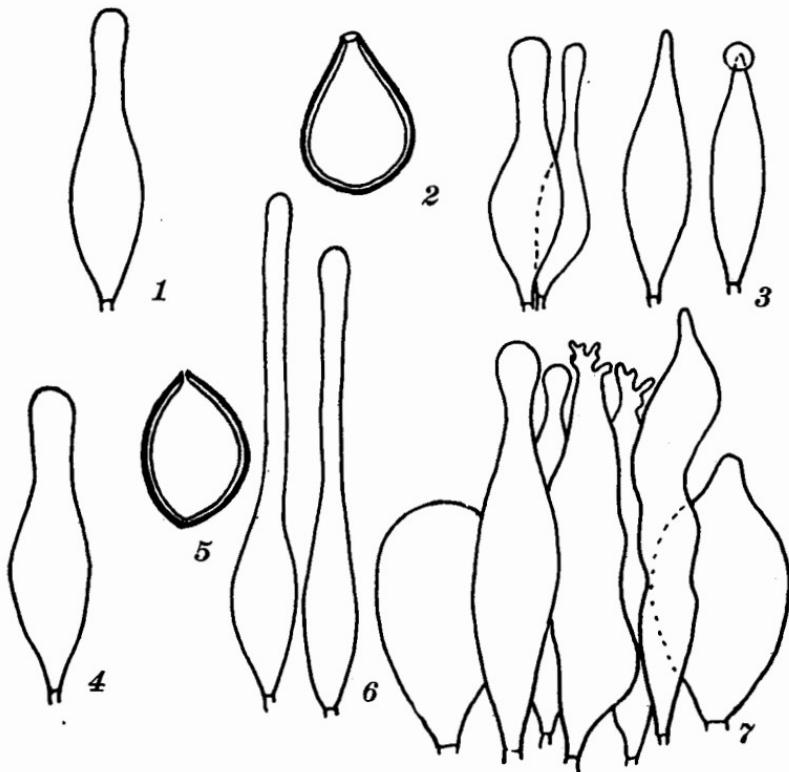


Plate 69

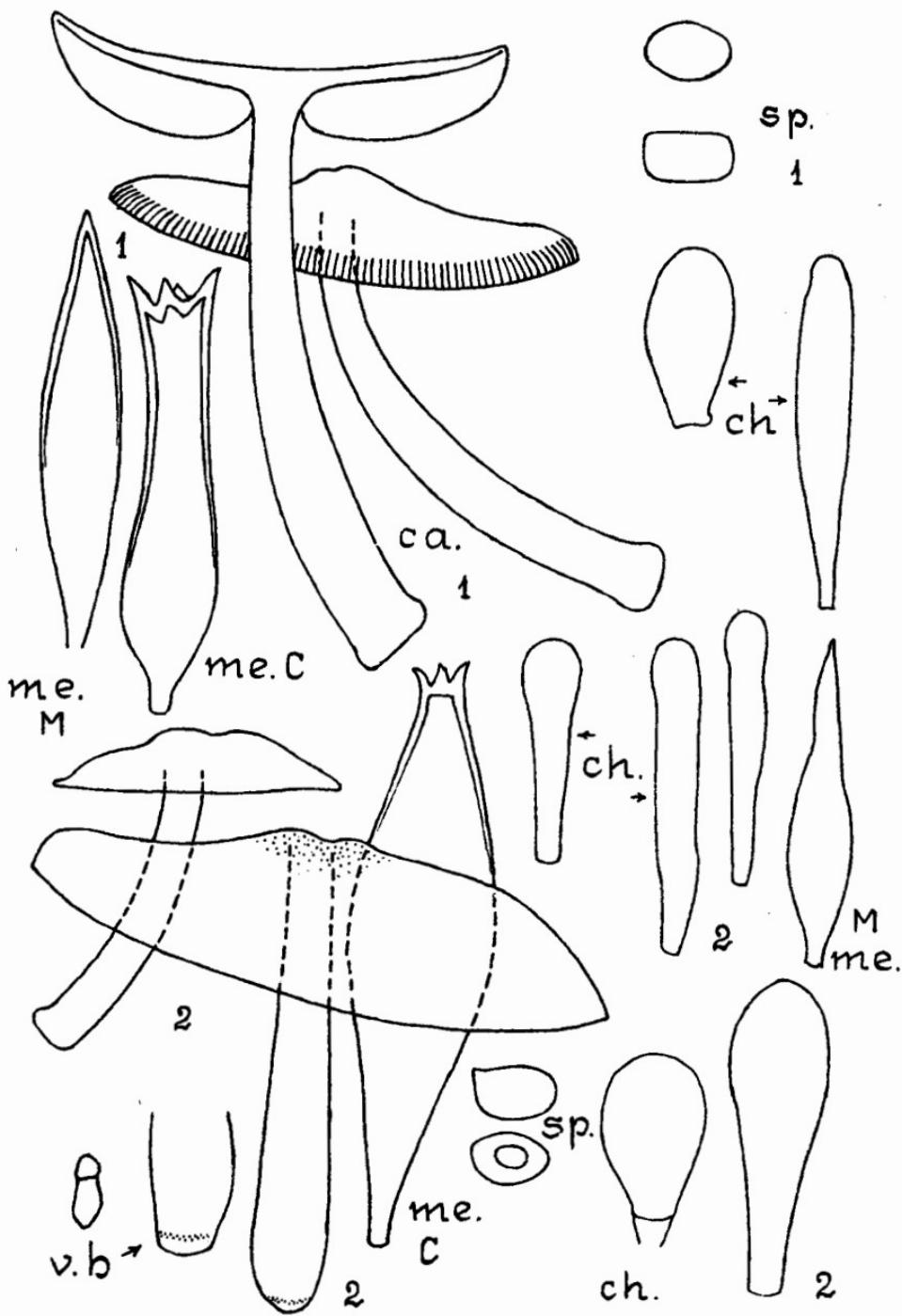


Plate 70

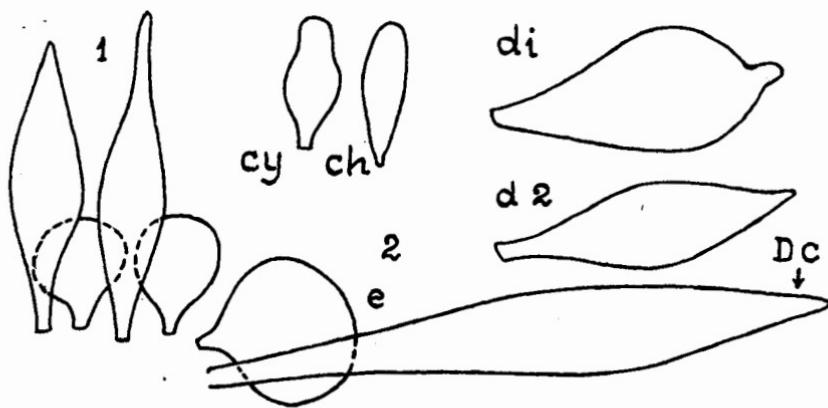
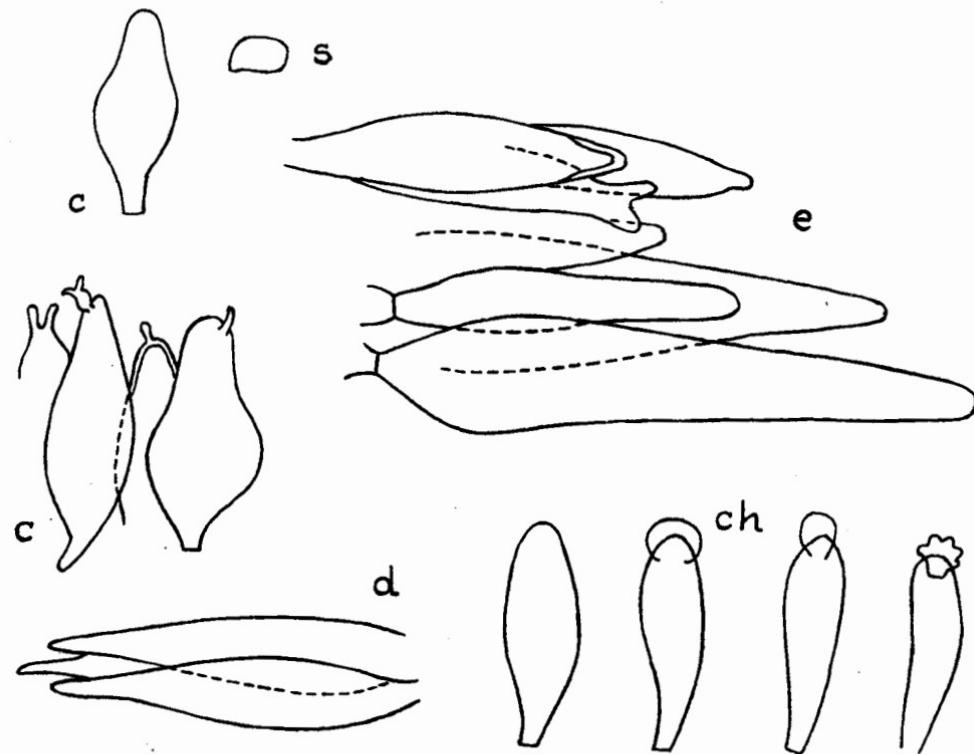


Plate 71

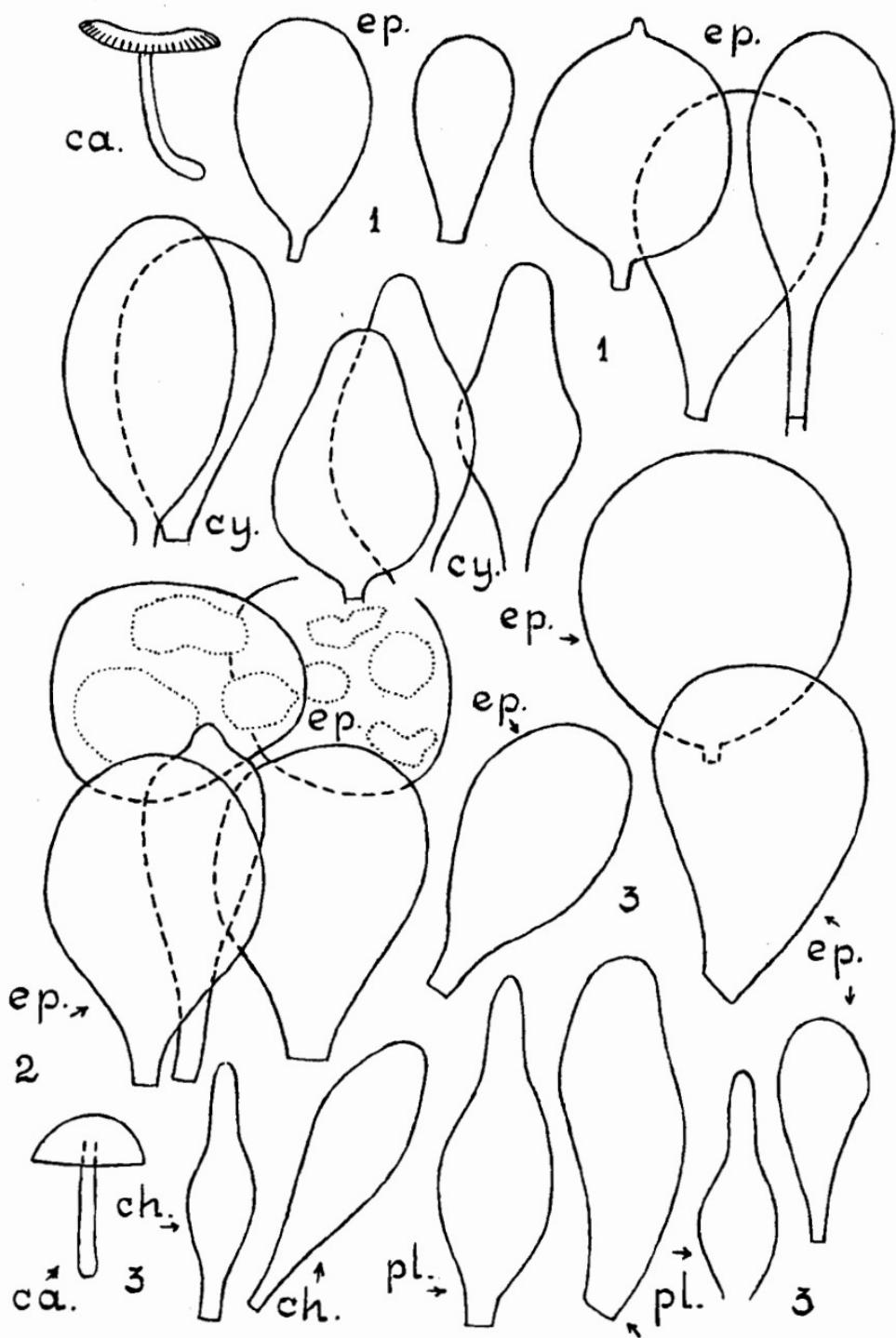


Plate 72

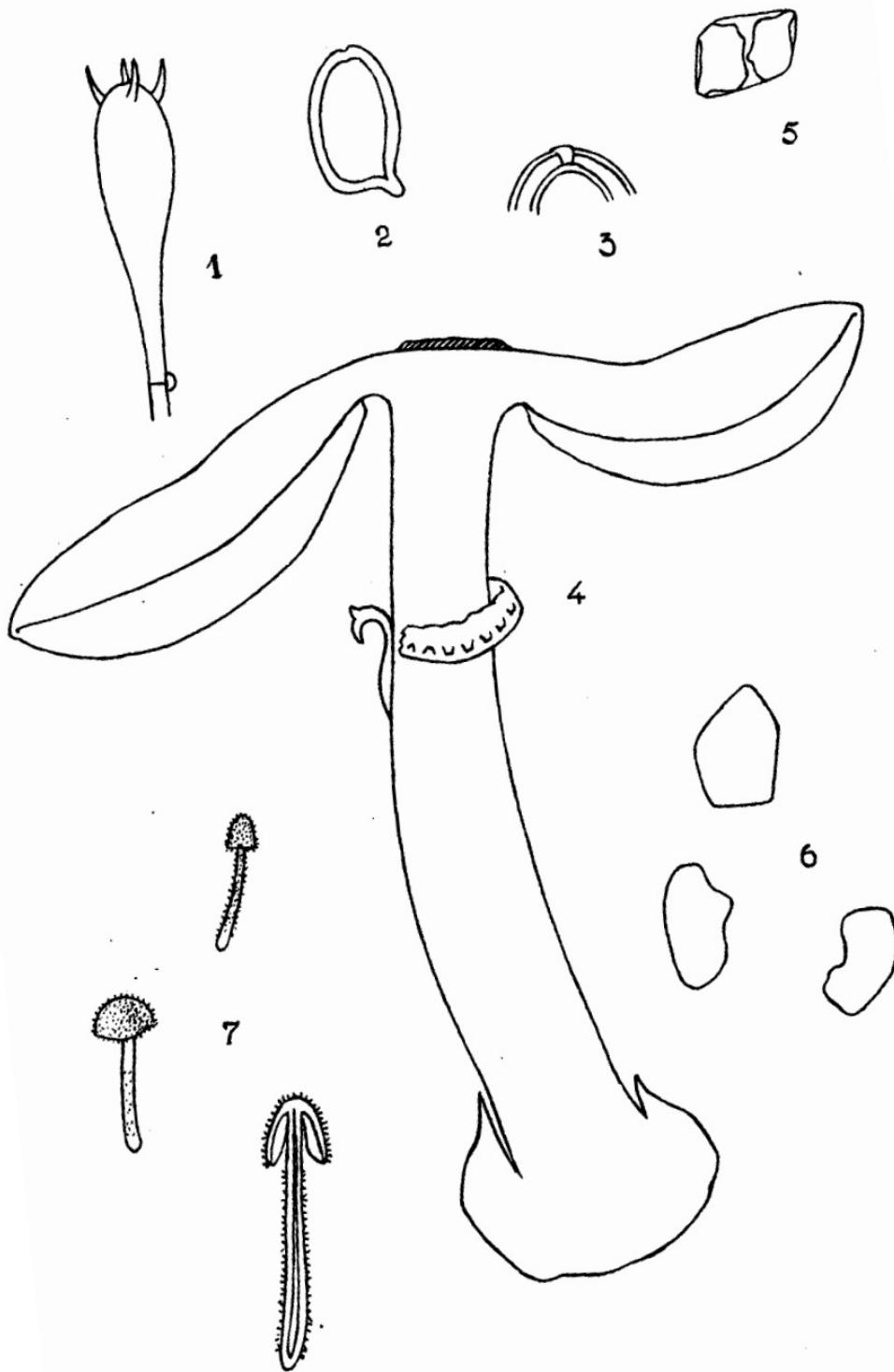


Plate 73

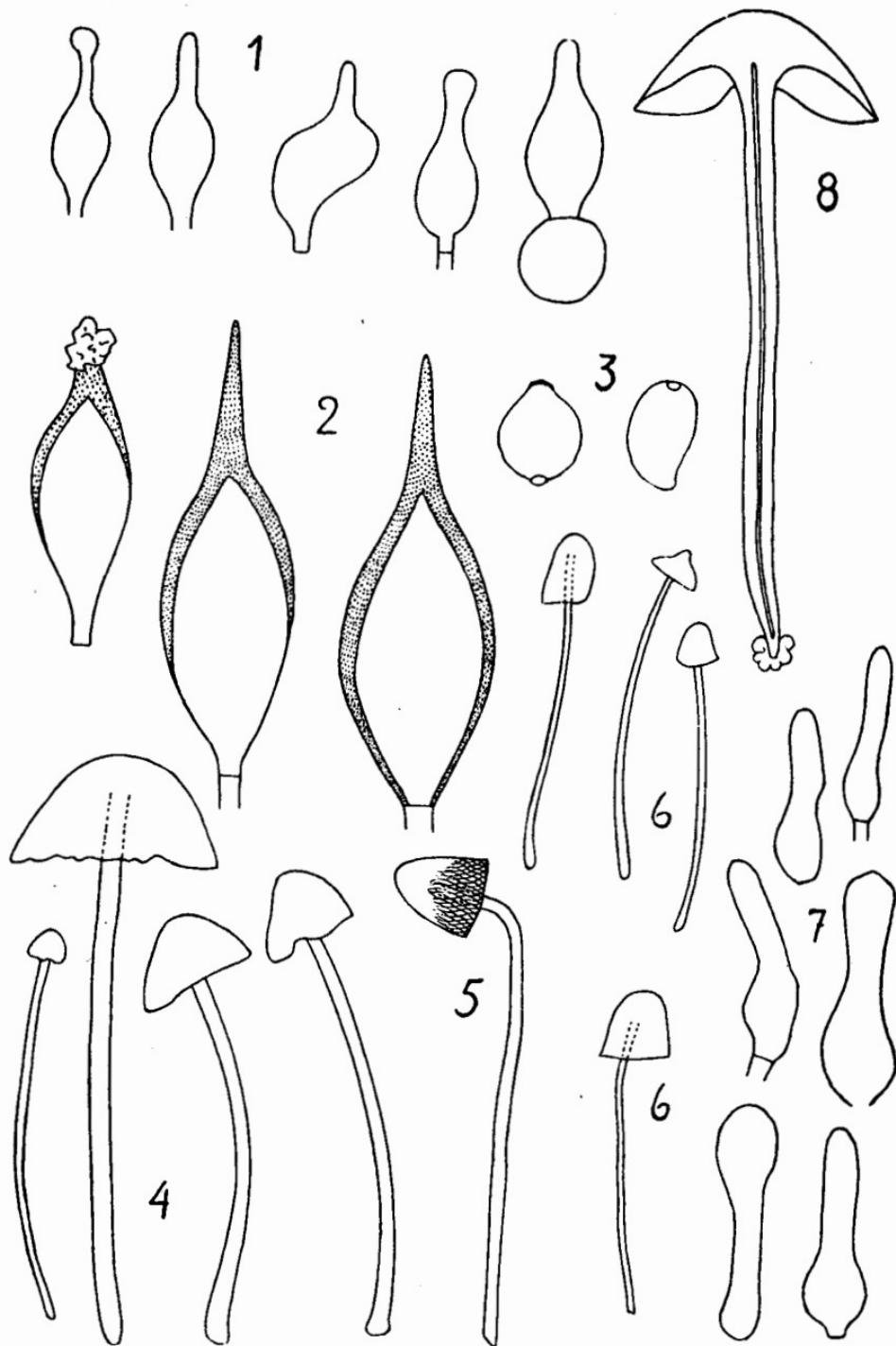


Plate 74

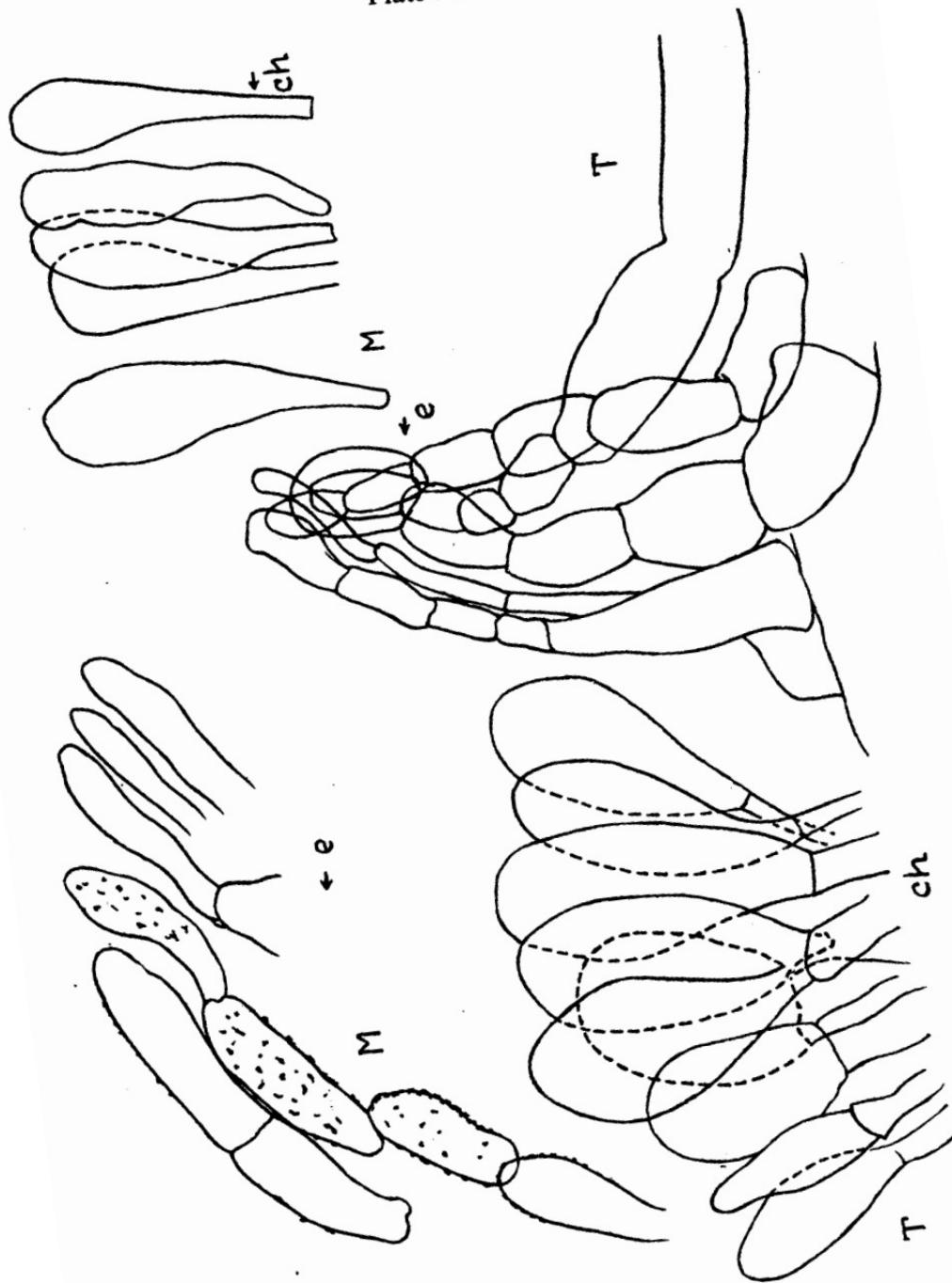


Plate 75

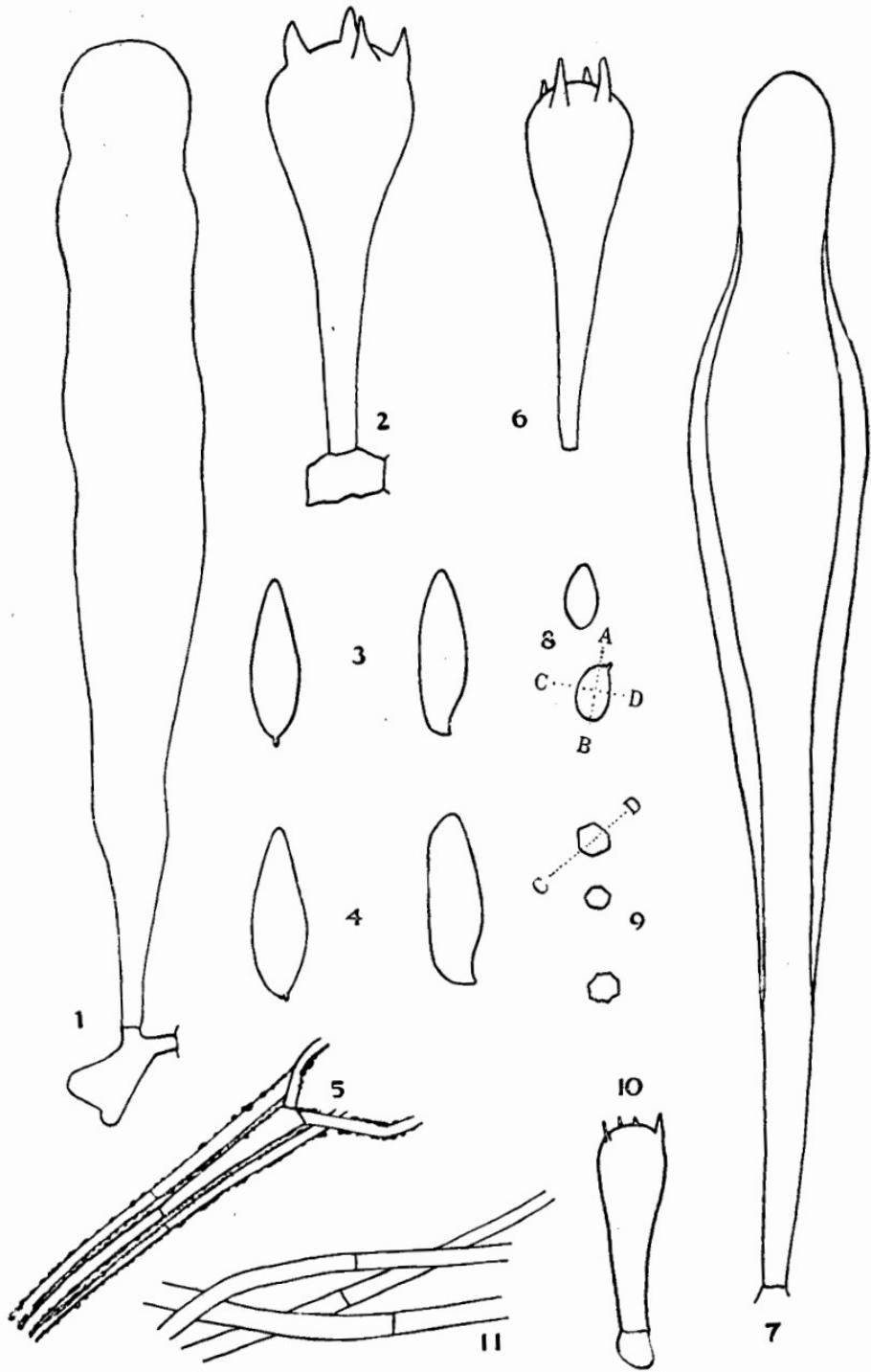


Plate 76

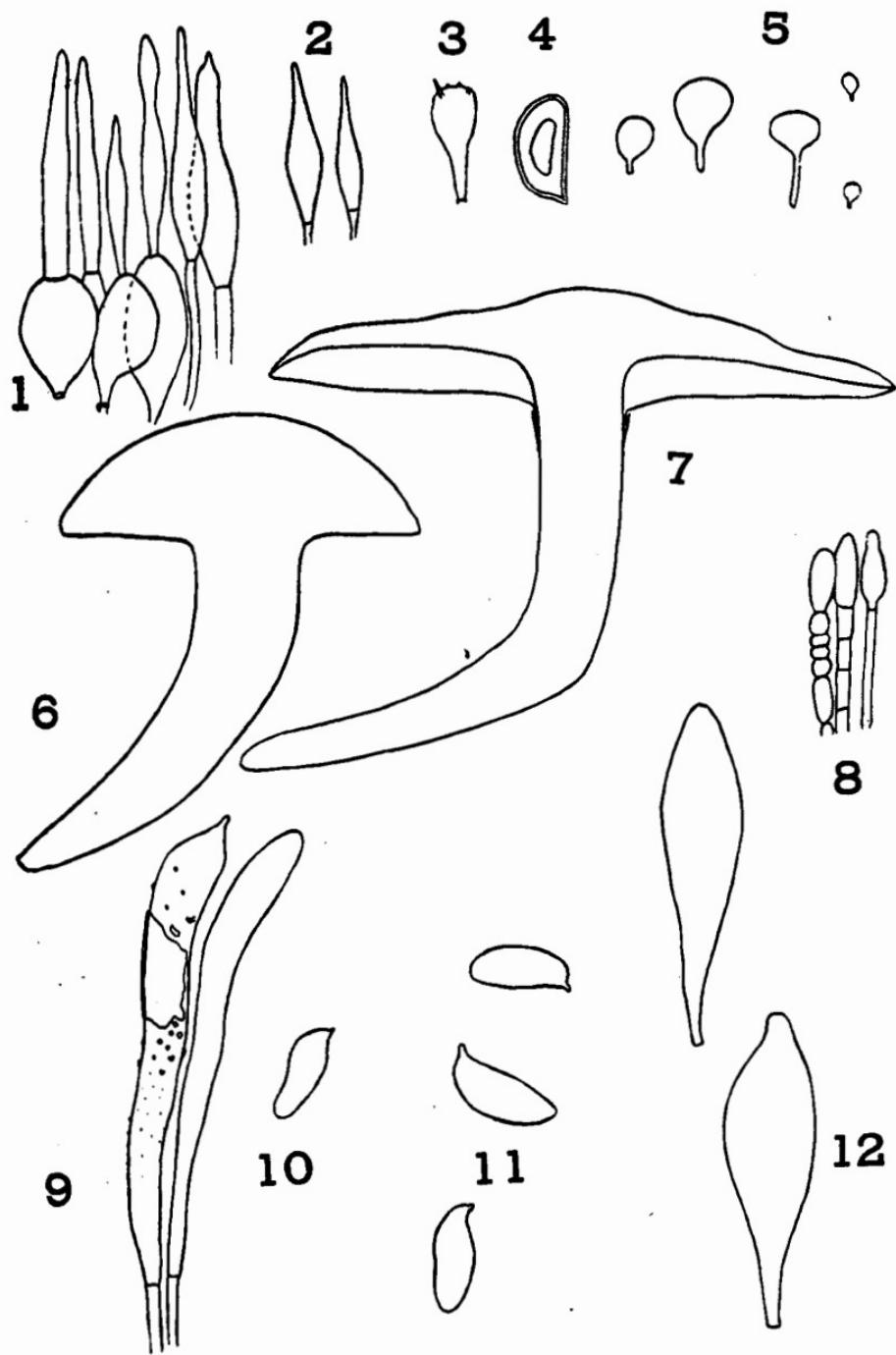
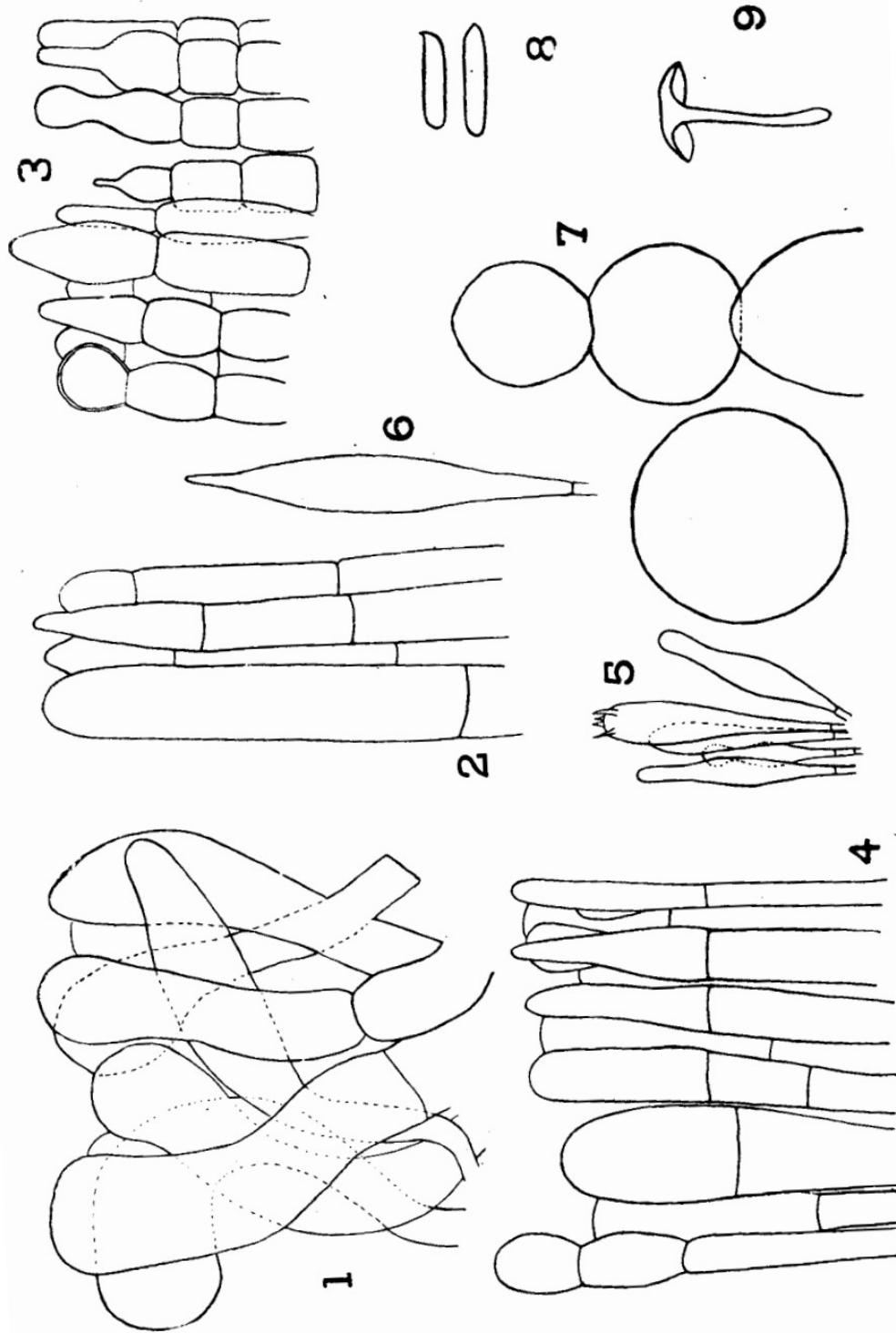


Plate 77



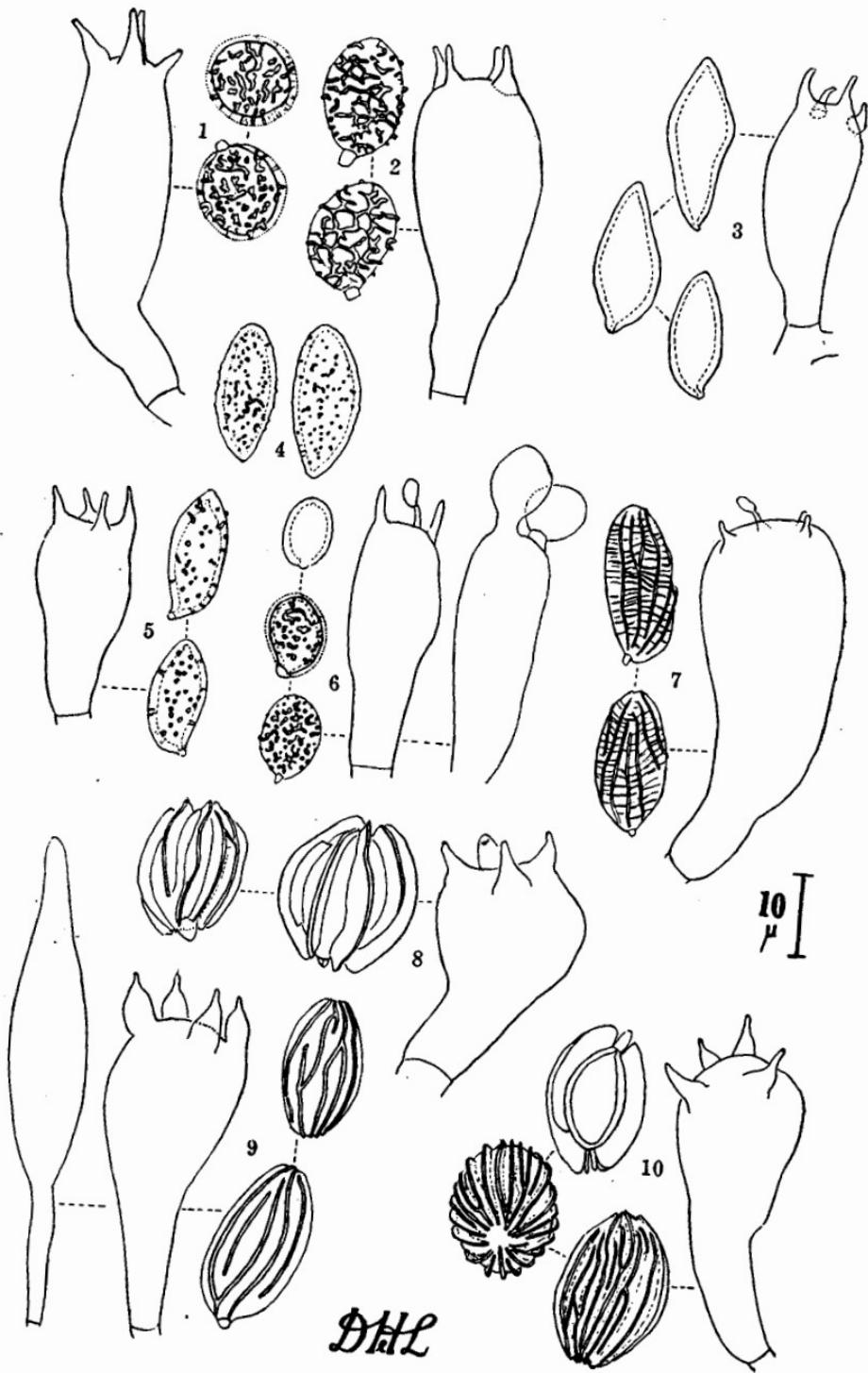


Plate 79

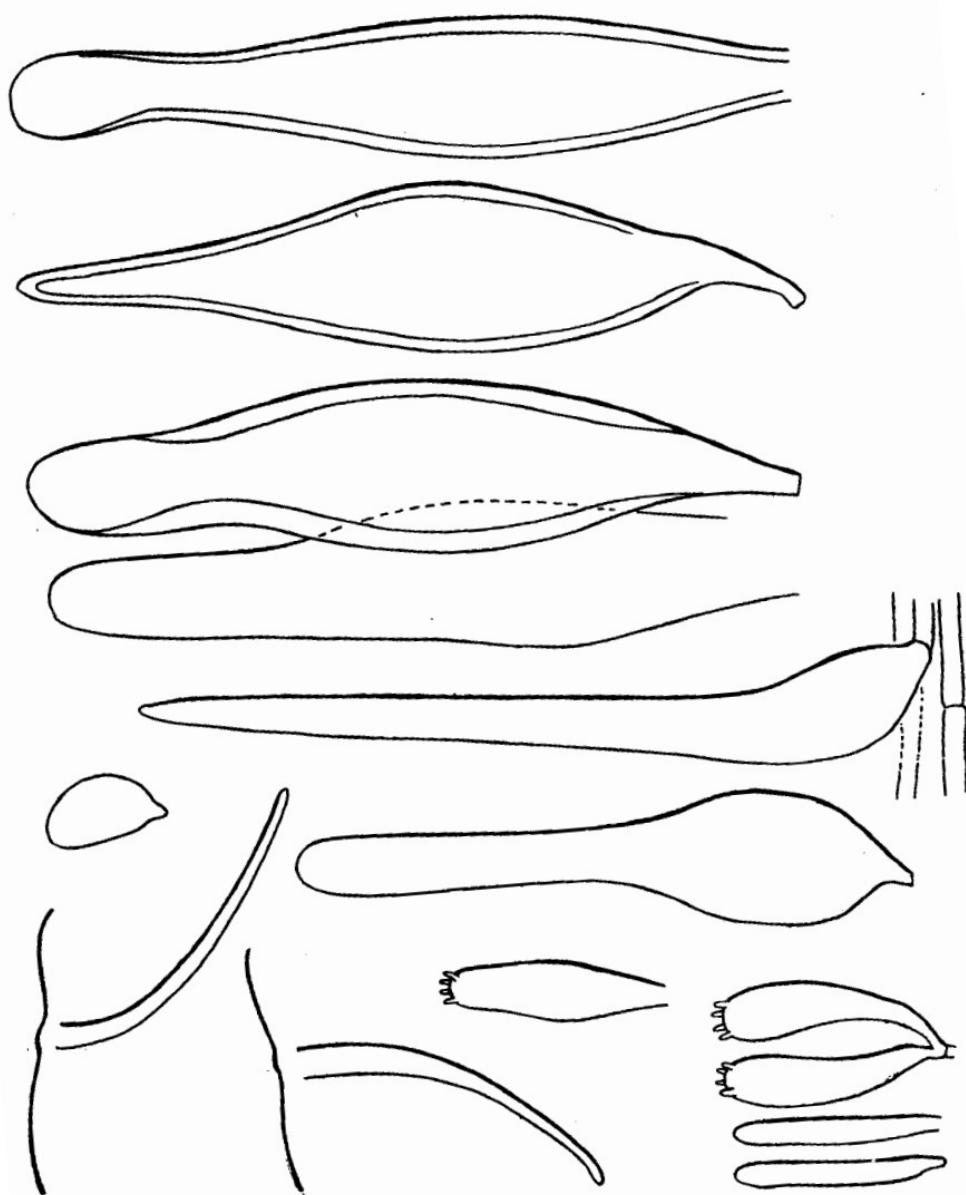


Plate 80

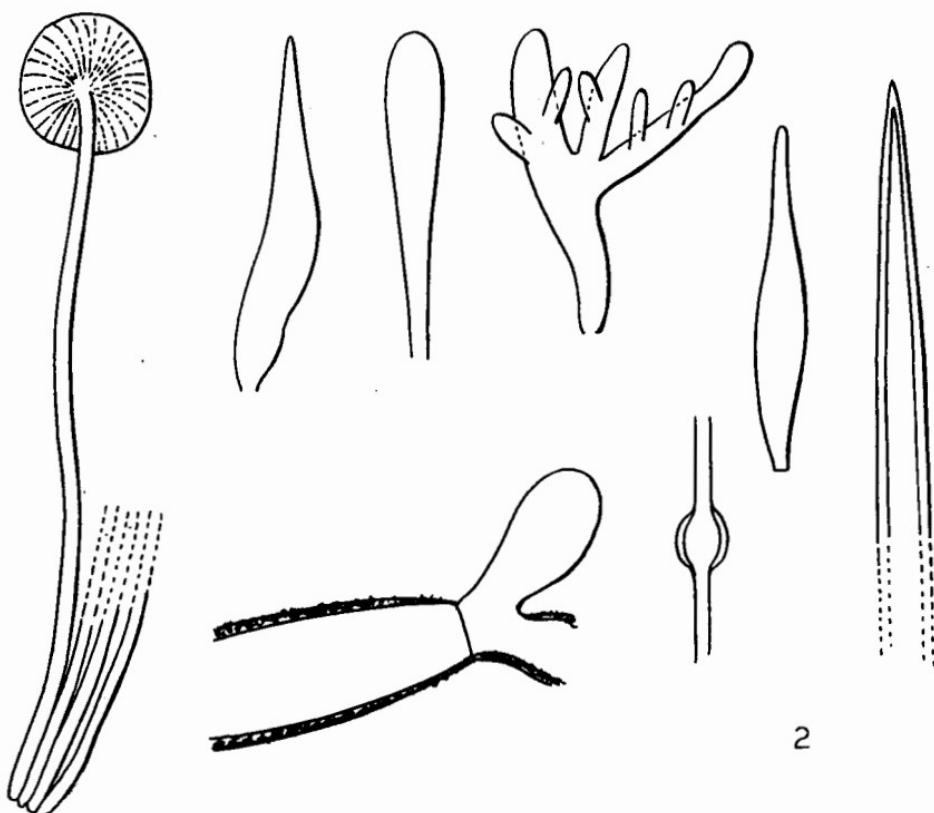
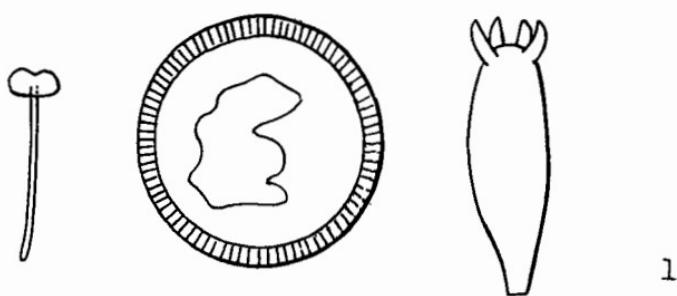


Plate 81

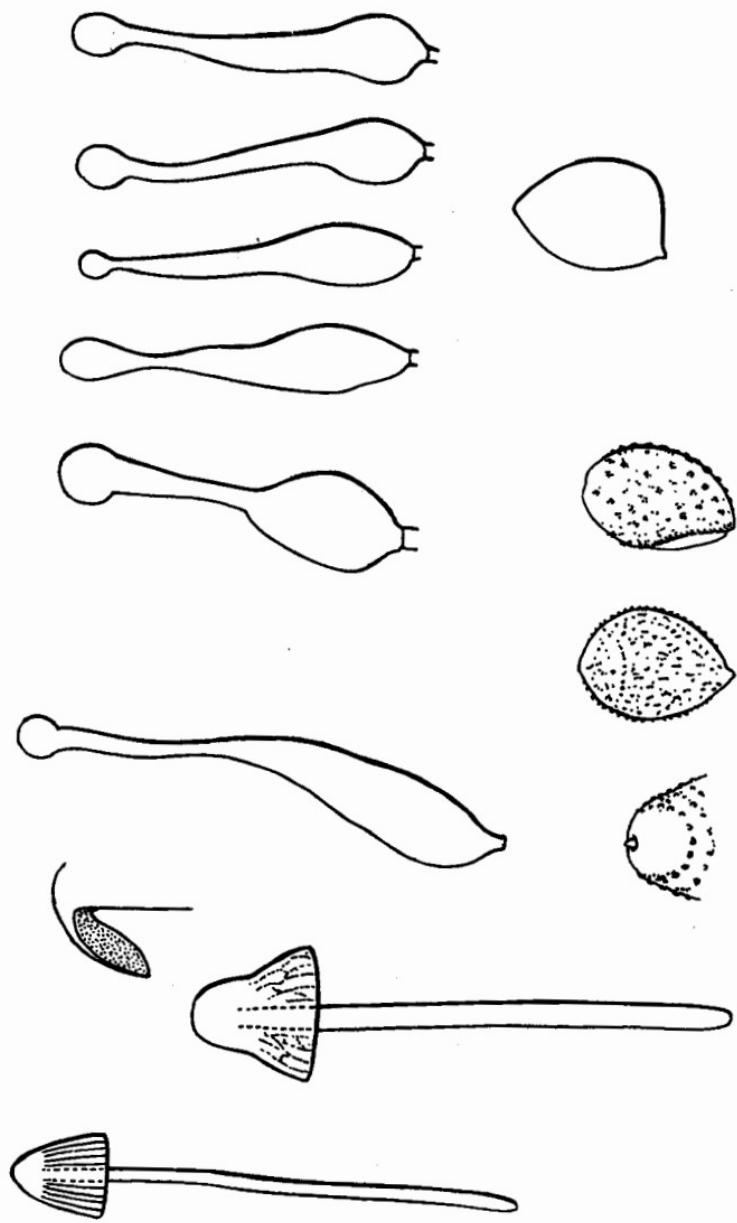


Plate 82

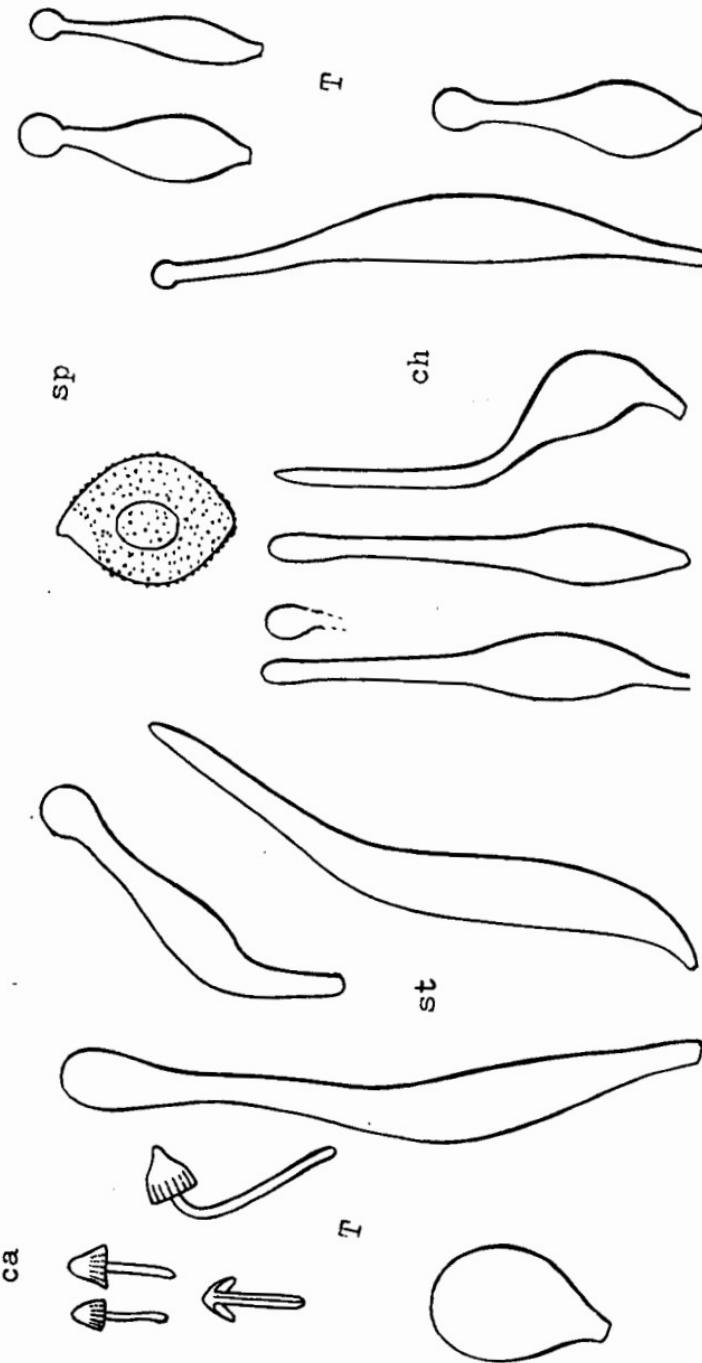
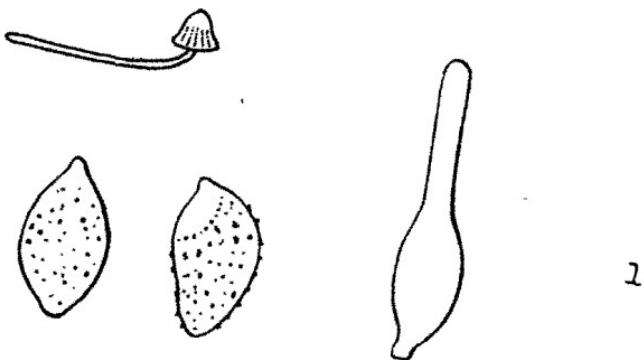


Plate 83



2

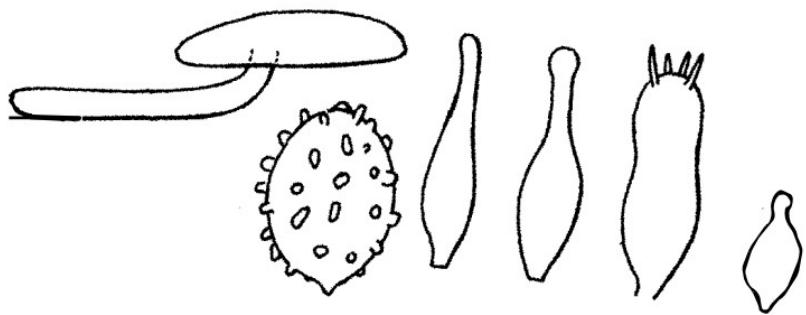
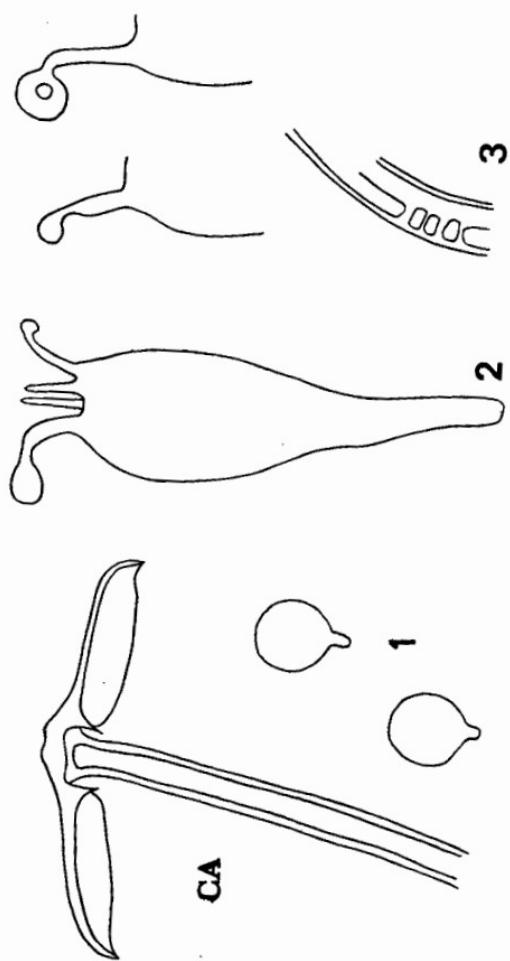
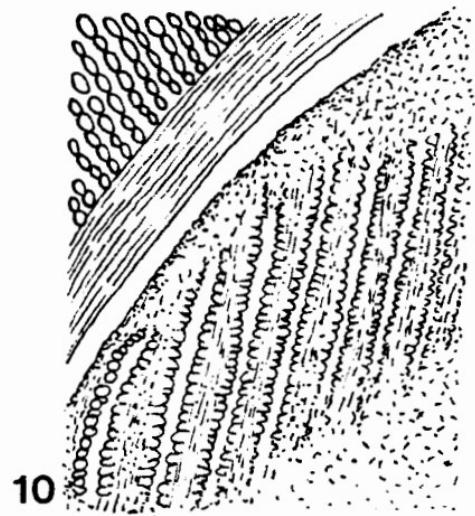
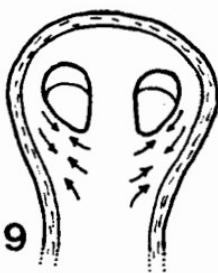
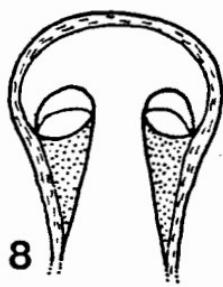
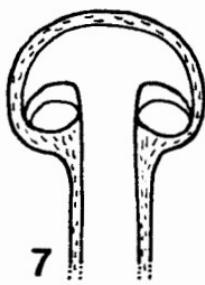
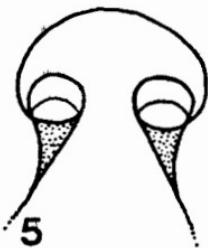
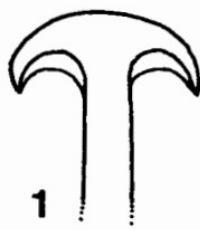
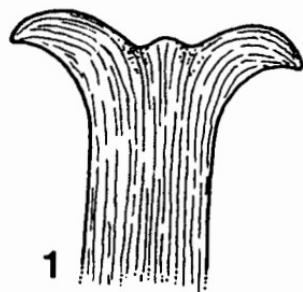


Plate 84



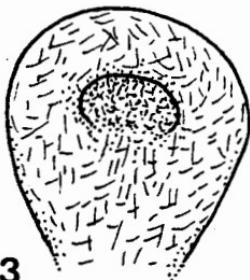




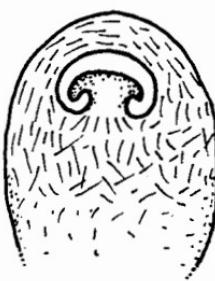
1



2



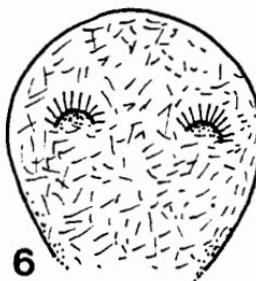
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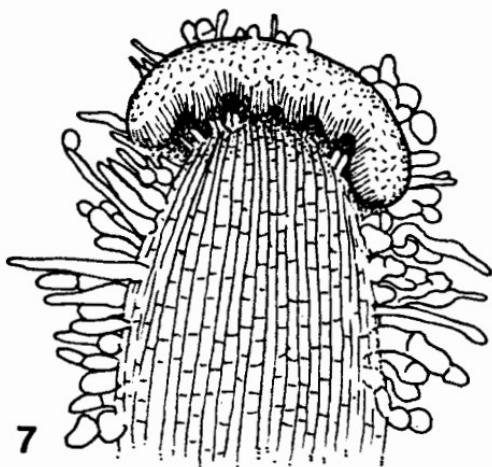
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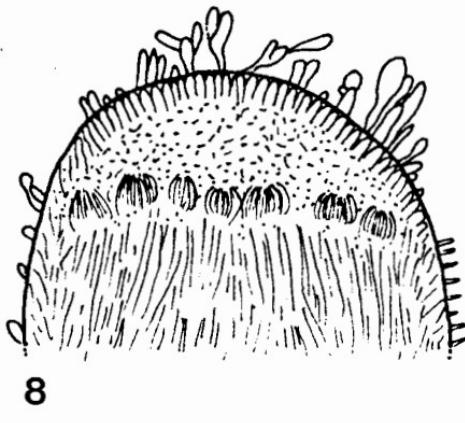
5



6



7



8

Plate 87

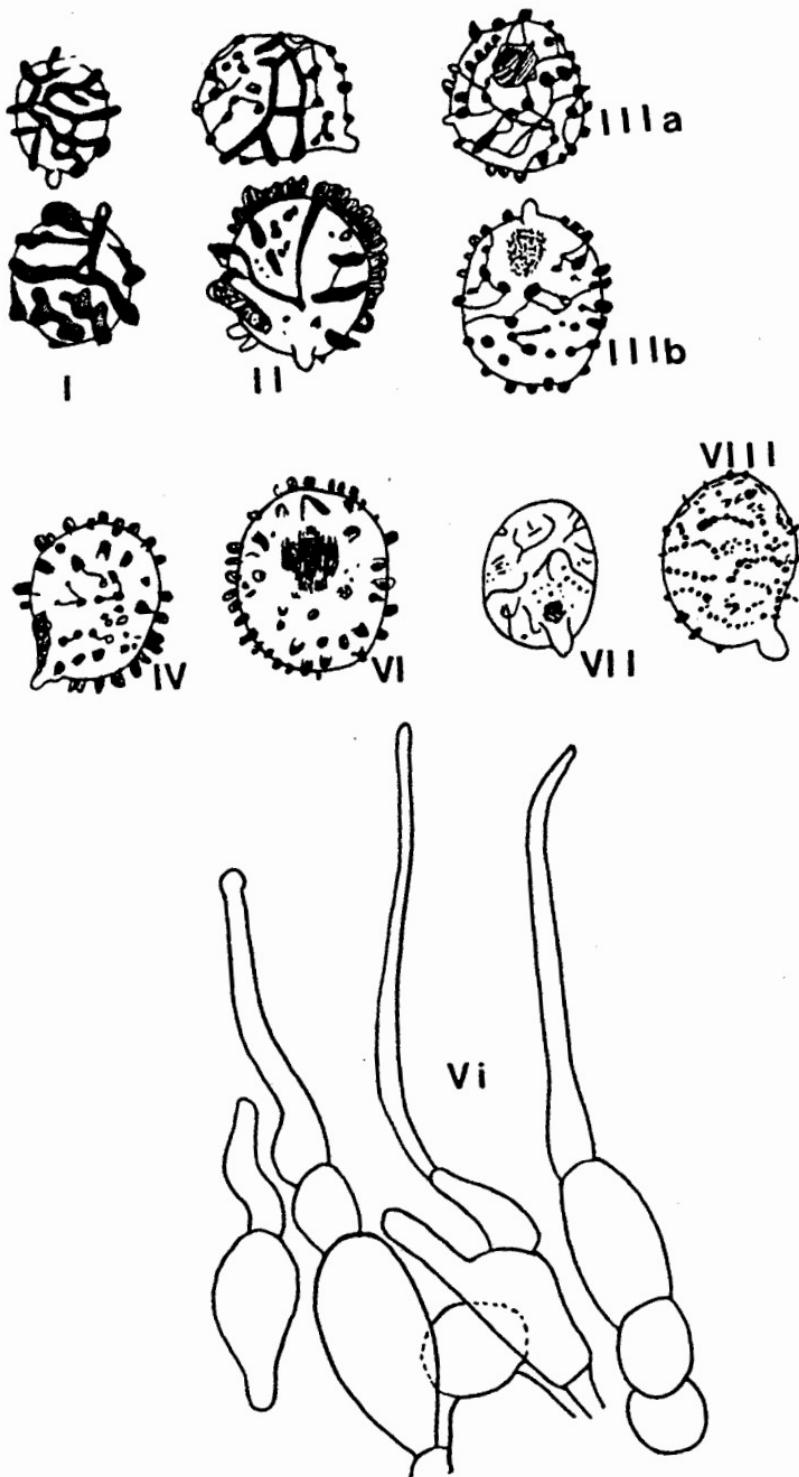


Plate 88

